

AN ABSTRACT OF THE THESIS OF

Nicolas Romero for the degree of Master of Science in Fisheries Science presented on December 19, 2003.

Title: Seasonal Influences on Food Availability and Diet of Coastal Cutthroat Trout in Relation to Riparian Vegetation.

Abstract approved: _____

Robert E. Gresswell

Judith L. Li

Current riparian management objectives in the Pacific Northwest promote both retention of existing conifers and conversion of hardwood-dominated areas to conifers. Although understanding of relationships between riparian vegetation and salmonid prey availability is growing, temporal variation in these relationships is poorly understood. Seasonal fluxes in availability of aquatic and terrestrial invertebrate prey for coastal cutthroat trout (*Oncorhynchus clarki clarki*) were investigated by estimating invertebrate biomass from aquatic (benthos and drift) and allochthonous (terrestrial) sources in three watersheds in the Oregon Coast Range. To investigate the influence of vegetation type on food sources, samples were collected in each watershed from stream sections dominated by deciduous, conifer, and mixed vegetation. During each sample period, diet was assessed by examining gut contents of captured trout. Stream discharge appeared to be an influential factor regulating seasonal fluxes of aquatic invertebrate biomass in the benthos and drift. Total

allochthonous invertebrate biomass at deciduous and mixed vegetation sites (64 and 61 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, respectively) was almost 30% higher than at coniferous sites (45 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$). Although aquatic insects dominated the total gut contents during this study, prey from terrestrial origin was more common during summer and fall. These results suggest that systematic removal of deciduous vegetation in riparian zones to promote conifers may have unintended consequences on the food resources of coastal cutthroat trout and the productivity of aquatic food webs in the Pacific Northwest.

**Seasonal Influences on Food Availability and Diet of Coastal Cutthroat Trout in
Relation to Riparian Vegetation**

by
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APPROVED:

Co-Major Professor, representing Fisheries Science

Co-Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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**Seasonal Influences on Food Availability and Diet of Coastal Cutthroat Trout in
Relation to Riparian Vegetation**

CHAPTER 1: INTRODUCTION

In the Pacific Northwest large conifers are valued in riparian ecotones for maintaining habitat and water quality for salmonid persistence. Because decomposition rates of coniferous wood in streams are significantly lower than those of wood input from deciduous species (Harmon et al. 1986), persistence of large conifer logs increases organic matter and sediment retention (Speaker et al. 1984; Gregory et al. 1991), provides habitat stability for fish (Gregory et al. 1991), and maintains light and thermal regimes (Johnson and Jones 2000). As these riparian functions are commonly associated with salmonid persistence, current riparian management objectives tend to promote both retention of existing conifers and conversion of hardwood-dominated areas to conifers (USDA 1996; ODF 1998). However, deciduous vegetation in headwater streams of the Oregon Coast Range dominates the near stream (15 m) riparian community (Nierenberg and Hibbs 2000). Because these regulations are relatively new, it is unclear the effect this conversion may have on habitat quality for fish.

In contrast to these physical effects on fish habitat, only limited information exists about what terrestrial plant communities contribute to aquatic food webs. In forested streams, the phenology of allochthonous deciduous material is important to the structure and function of aquatic food webs (Petersen and Cummins 1974; Cummins et al. 1989). For example, deciduous plant litter is especially important as a nutritional resource for aquatic organisms (Bobcock 1964; Iversen 1974). Nitrogen, an essential nutrient for microbial and invertebrate protein, is present in greater quantities in

rapidly decomposing red alder (*Alnus ruba*) leaves than in more slowly decomposing needles of coniferous species (Triska et al. 1975). Furthermore, microbial colonization of leaf litter, along with its subsequent invertebrate utilization, occurs more rapidly in red alder leaves than in conifer needles (Sedell et. al 1975). Because deciduous plant litter is preferred by aquatic detritivores (Iversen 1974; Hieber and Gessner 2002), an abundance of these plants may increase aquatic prey for fish for much of the year.

In some headwater systems invertebrates associated with terrestrial vegetation are important sources of food for salmonids (Wipfli 1997; Kawaguchi and Nakano 2001; and Allan et al. 2003). For example, terrestrial invertebrate inputs represent an important component to fish diets (Mason and MacDonald 1982; Cloe and Garman 1996; Wipfli 1997). Terrestrial arthropods that accidentally fall into stream channels represent a high quality food resource directly available to fishes, and these organisms can comprise more than 50% of salmonid diets during some seasons (Hunt 1975; Wipfli 1997). Because deciduous plants can support greater terrestrial arthropod biomass per stem than conifers (Allan et al. 2003), they potentially contribute more food for fish (Wipfli 1997).

Although our understanding of the relationships between riparian vegetation type and salmonid prey availability is growing, numerous questions remain unanswered. For example, how do invertebrate biomass and species composition vary among stream sections with differing vegetative composition? Does the diet of salmonid

fishes vary seasonally in these riparian communities? Is fish condition (i.e., plumpness) related to prey consumption?

The goal of this study was to examine seasonal influences of riparian vegetation on aquatic food webs in headwater streams of forested areas of the Oregon Coast Range. Specifically, we (1) compared invertebrate biomass and species composition from benthic, drift, and allochthonous sources among stream sections with deciduous-dominated, conifer-dominated, and mixed (deciduous-conifer) vegetation, (2) determined seasonal variation in prey availability and diet of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in these riparian communities, and (3) examined fish condition in relation to prey consumption.

CHAPTER 2: STUDY AREA AND METHODS

Study Area

The study was conducted June 2001-April 2002 in sections of three headwater streams in the Oregon Coast Range. Sites were located above barriers to anadromous fishes in order to avoid the potential confounding effect of marine derived nutrients from salmon carcasses. Coastal cutthroat trout were the only salmonid present in these areas during the study. Study sites were located on Camp Creek, a tributary to the Umpqua River; Tucca Creek, a tributary to the Nestucca River; and North Fork Ecola Creek, which flows directly into Pacific Ocean (Fig. 1). In each stream there were three study sections; each study section represented one of three riparian vegetation types (deciduous, conifer, and mixed) (Fig. 1).

On Camp Creek (43° 50' N, 123° 53' W), study sections were all located in portions of the watershed managed by the U.S. Bureau of Land Management (BLM). Since 1940, timber harvest has occurred in approximately 51% of the watershed, mainly in the upper portions of tributaries and ridge tops (BLM 1995). Old-growth (exceeding 200 years old) Douglas-fir (*Pseudotsuga menziesi*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), sword fern (*Polystichum munitum*), salmonberry (*Rubus spectabilis*), and vine maple (*Acer circinatum*) are present throughout the riparian corridor (BLM 1995). Currently, the upper 10 km of the Camp Creek watershed, including the study area, is designated as a late-successional reserve

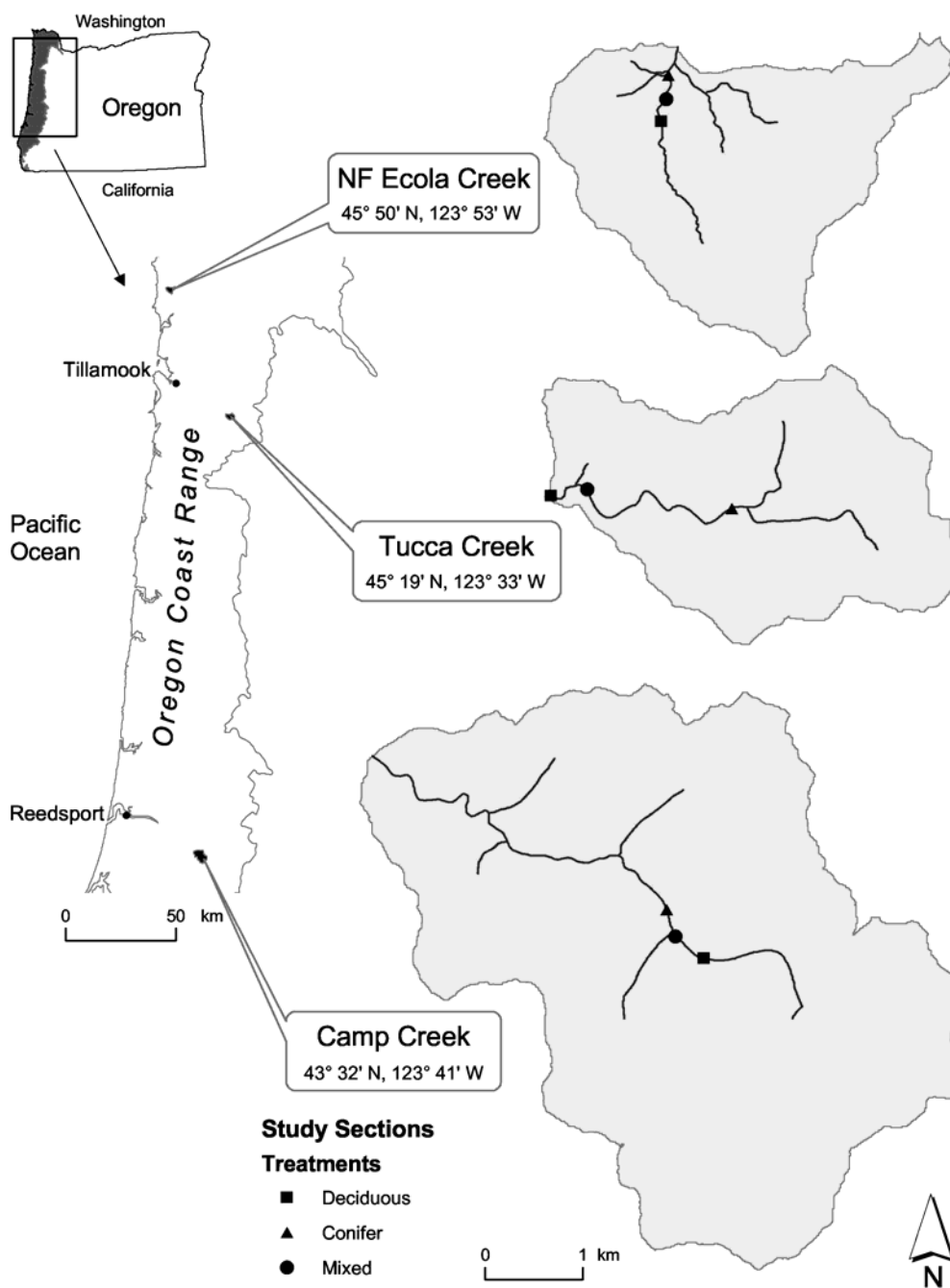


Figure 1. Location of streams sampled and sites within streams in the Oregon Coast Range, U.S.A.

(management objective is to protect and enhance conditions of late successional and old-growth forest ecosystems) and is being managed to achieve late-successional characteristics (BLM 1995).

Study sites on Tucca Creek (45° 19' N, 123° 33' W) were also located on land administered by the BLM. Large fires in the late 1800s, 1933, 1939, and 1945, and subsequent salvage operations and timber management activities have created a relatively homogeneous forest. The majority of stands in this area are 40 to 60 years of age (BLM 1994). Timber along intermittent portions of the stream has been harvested during the last 10 years; however, the conifer study section contained Douglas fir, western hemlock, and western red cedar that were >100 years old (Fig. 1). Currently, the entire Tucca Creek watershed (800 ha) is being managed to achieve late-successional characteristics (BLM 1994).

North Fork Ecola Creek (45° 50' N, 123° 53' W) flows directly into the Pacific Ocean. Weyerhaeuser Company owns the majority of the watershed. Approximately 95% of the North Fork Ecola Creek watershed is managed as commercial forestland, and at the time of the study, vegetation was dominated by 50 year-old even-aged western hemlock and Sitka spruce (*Picea sitchensis*) (Parker 2001). The riparian overstory canopy in North Fork Ecola Creek was primarily western hemlock and Sitka spruce dominant and red alder was sparse. Additional trees and shrubs present in the riparian zone include western red cedar, grand fir, Douglas fir, vine maple, salmonberry, and huckleberry (*Vaccinium sp.*).

Riparian Habitat Survey and Abiotic Measurements

The length of an individual study section varied from 10-15 active channel widths. This method provided a relative length based on channel morphological characteristics. To quantify riparian canopy cover and composition in the nine study sections, we measured vegetation along three 50-m transects perpendicular to stream flow at the one-quarter, half, and three-quarter distance from the downstream end of each study section. Along each transect we measured overstory cover using a moosehorn at 15 sample points (stream center, wetted edge, bankfull, and every 5 m out to 25 m from each bankside) (Bonnor 1967). To characterize riparian understory we visually estimated shrub cover and composition in 5 m radius plots set along transects perpendicular to stream flow at stream center, 5 m, 10 m, and 20 m locations on each bank.

Water temperature, air temperature, and stream discharge were measured throughout the study. A temperature data logger (Optic StowAway, Onset Computer Co.) was placed in each study section to record hourly water temperature, while an additional data logger (Hobo, Onset Computer Co.) was deployed to record hourly air temperature. Stream discharge ($\text{m}^3 \cdot \text{sec}^{-1}$) was measured in each section during each sample period with a flow meter (Marsh McBirney Model 2000) by methods described in McMahon et al. (1996).

Invertebrate Prey Availability

To examine seasonal fluctuations in prey availability, estimates of invertebrate biomass and composition from benthic, drift, and allochthonous sources were obtained four times during the study: summer (July 06 – August 08, 2001), fall (October 01 – October 23, 2001), winter (January 10 – February 20, 2002), and spring (April 02 – April 19, 2002). Benthic invertebrates were collected once each season with a 500- μm mesh Surber sampler (0.09 m^2 area) at 6 random locations in riffle habitat of each study section. Invertebrate drift was estimated by concurrently placing one drift net (500- μm mesh; $0.4\text{ m} \times 0.4\text{ m}$ opening at the mouth) in the thalweg of riffle habitat at each end of a study section for 20 minutes at dawn. Drift nets were positioned to intercept total water column and capture invertebrates floating on the water surface.

During each study period, arthropod inputs were estimated from samples collected in pan traps (0.056 m^2) for 7 days. Twelve pan traps in each study section were suspended 1 m above the water surface on metal rebar stands. Pan traps were filled with 3 cm of water and two to three drops of surfactant to retain captured invertebrates. The wetted channel area was divided longitudinally into 3 subsections (left, center, and right); four pan traps were placed randomly in each subsection (Doolittle and Starkey, 2002). Pan trap contents were sieved (225- μm mesh) at the completion of each 7-day sample period and preserved in 95% ethanol alcohol solution until analyzed.

Invertebrates collected from the benthos, drift, and pan traps were sorted under a dissecting microscope, taxonomically identified (primarily to the family level),

enumerated, and measured to the nearest 0.5 mm using an eyepiece micrometer.

Invertebrates were categorized as terrestrially derived or aquatically derived based on environment type of the larval stage (Wipfli 1997). Macroinvertebrate biomass was estimated with published taxon-specific length-mass regression equations (Sample et al. 1993; Hodar 1996; Benke et al. 1999).

Benthic invertebrate biomass estimates from Surber samples (dry mass $\text{mg}\cdot\text{m}^{-2}$) were combined to obtain the mean for all samples in a study section by sample period. Allochthonous invertebrate biomass estimates from pan trap samples (dry mass $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) were also combined to obtain the mean for all samples in a study section by sample period. Drift biomass (dry mass $\text{mg}\cdot\text{m}^{-3}$) was calculated by dividing the weighed dry mass of invertebrates retained per net by the estimated water volume moving through each net during the sample period. Drift biomass rate (dry mass $\text{mg}\cdot\text{m}^{-3}\cdot\text{hour}^{-1}$) for each study section in a sample period was estimated by multiplying the total value of the upstream and downstream net biomass estimates (dry mass $\text{mg}\cdot\text{m}^{-3}$) by water volume filtered ($\text{m}^3\cdot\text{hour}^{-1}$) and combining rates for each to obtain the mean (Kawaguchi and Nakano 2001).

Coastal Cutthroat Trout Diet

Coastal cutthroat trout were sampled during each study period to collect stomach contents. During each sample period, we allowed 24 h for habitat to recover from disturbance associated with instream invertebrate sampling and coastal cutthroat trout to return to natural foraging behavior. A variable wave-form backpack electrofishing

unit (Model 12, Smith-Root Inc., Vancouver, USA) was used to capture coastal cutthroat trout. Electrofishing occurred between 1000 and 1600 hours. Collection proceeded upstream until 20 coastal cutthroat trout were captured in each study section. Fish were placed in 20-L buckets of water and anesthetized with a solution of water and clove oil (Keene et al. 1998). Stomach contents were removed by flushing procedure with a narrow pipeted water bottle and strained into paper coffee filters, and placed into small plastic bags filled with 95% ethanol alcohol (Meehan and Miller 1978). Only stomachs of coastal cutthroat trout ≥ 80 mm (total length) were sampled, and time and location of capture and total length (to nearest 1 mm) and weight (to nearest 0.1 gram) were recorded for each fish. Subsequently, all fish were returned to their original capture location when fully recovered.

Invertebrates from stomach contents were preserved in 95% ethanol solution. In the lab, organisms were taxonomically identified to family when possible, origin was categorized, and each individual was measured (to the nearest mm) for estimating biomass from length-weight regressions (Sample et al. 1993; Hodar 1996; Benke et al. 1999). Lengths of partially digested prey were estimated from intact individuals of the same taxon that appeared to be similar in size (Wipfli 1997). The biomass of invertebrates ingested by all individual fish was combined to obtain the mean for each study section and season.

Coastal Cutthroat Trout Condition Factor

Relative condition factor (K_n) was used to assess cutthroat trout condition (Anderson and Neumann 1996). Relative condition factor was calculated as:

$$K_n = (W/W'),$$

where W is the weight of an individual, and W' is the length-specific mean weight predicted by a weight-length regression for cutthroat trout captured in this study. The length-specific mean weight (W') was calculated as:

$$\log_{10}(W') = a' + b \cdot \log_{10}(L),$$

where a' is the intercept value and b is the slope of the regression equation, and L is the total length of the fish (Anderson and Neumann 1996). The weight-length regression for coastal cutthroat trout sampled in this study was:

$$\text{Log}_{10}(W') = -4.9447 + 2.9511 \cdot \log_{10}(L)$$

Fish of average condition are described by a K_n value of 1.0. K_n values below 1.0 suggest low condition and fish with K_n values above 1.0 describe fish in good condition relative to other individuals in the population.

Statistical Analysis

Repeated measures analysis of variance was used to compare invertebrate availability and fish diet among riparian vegetation types and season. Biomass estimates of invertebrate availability (benthic, drift, and pan-trap samples) and prey mass ingested were analyzed according to a split-plot design where riparian vegetation type (deciduous, conifer, and mixed) was the treatment and sites on the three streams

were the experimental units that were measured seasonally (July-August 2001, October 2001, January-February 2002, and April 2002). The same study design was used to analyze fish condition in each of the riparian vegetation, stream, and season combinations. Biomass data were transformed (\log_{10}) to standardize variances and to meet the normality assumptions of ANOVA. Multiple means comparisons were made using Tukey-Kramer procedures. A α value of 0.05 was used for statistical significance for all tests. Statistical differences between the mass of aquatic and terrestrial prey ingested within seasons were determined with *t*-tests. Pearson correlation coefficients were calculated to identify significant associations between invertebrate biomass (benthos, drift, and pan traps) and abiotic variables (stream discharge and air temperature) within each stream.

CHAPTER 3: RESULTS

Riparian Habitat Survey and Abiotic Measurements

Overstory trees along stream margins consisted primarily of red alder, big-leaf maple, Douglas fir, western red cedar, and Sitka spruce. Douglas Fir and red alder were common at most sites; however, sites at North Fork Ecola Creek were hemlock and Sitka spruce dominated and contained little red alder. Deciduous vegetation made $\geq 69\%$ of the overstory vegetation in deciduous and mixed sections at Camp Creek and the deciduous section at Tucca Creek (Table 1). Sites at North Fork Ecola Creek contained much less deciduous vegetation than Camp Creek and Tucca Creek. Although conifer sites in all streams contained some deciduous vegetation, the percentage of deciduous vegetation at conifer sites was lower than that found in deciduous or mixed sites. Sites on North Fork Ecola Creek contained lower percent canopy cover than Camp Creek and Tucca Creek sites (Table 1).

Sword fern (*Plystichum munitum*) was common and abundant at all sites. Salmonberry and vine-maple were common among sites at Camp Creek and Tucca Creek, but huckleberry and false azalea (*Menziesia ferruginea*) were common only to North Fork Ecola Creek. Conifer sites contained lower shrub cover than deciduous and mixed sites in all streams. Sites on North Fork Ecola Creek contained lower shrub cover than Camp Creek and Tucca Creek sites (Table 1). All sites contained pool-riffle channel morphology with gradients ranging from 2% to 5%. Active channel widths ranged from 5.0 to 9.5 m at deciduous sites, 6.2 to 9.7 m at conifer sites, and 8.6

Table1. Physical habitat and vegetation characteristics in stream study sections of Camp Creek, Tucua Creek, and North Fork Ecola Creek of the Oregon Coast Range. Numbers in parentheses indicate \pm standard error of the mean (SEM).

Variables	Camp Creek			Tucua Creek			Ecola Creek		
	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed
Drainage area (ha)	872	1158	903	800	417	686	229	257	250
Elevation (m)	253	244	248	427	524	439	311	317	320
Length (m)	160	190	115	120	150	180	105	102	155
Gradient (%)	2.0	1.5	2.2	2.8	3.4	2.5	5.0	3.6	3.7
Mean ACW ^a (m)	9.5 (0.44)	9.7 (0.57)	8.6 (0.43)	7.5 (0.50)	6.5 (0.48)	9.6 (0.54)	5.0 (0.39)	6.2 (0.52)	8.8 (1.1)
Mean discharge (m ³ •sec ⁻¹)	0.18 (0.12)	0.24 (0.17)	0.18 (0.12)	0.24 (0.13)	0.12 (0.17)	0.22(0.12)	0.19 (0.12)	0.20 (0.11)	0.19 (0.12)
Mean water (°C)	9.2 (0.4)	9.2 (0.04)	9.2 (0.4)	7.7 (0.02)	7.2 (0.02)	7.5 (0.02)	7.7 (0.02)	7.5 (0.02)	7.7 (0.02)
Canopy cover (%)	74.0 (4.0)	71.1 (4.9)	82.6 (3.5)	75.5 (4.0)	60.8 (4.9)	50.7 (5.7)	56.1 (5.3)	82.1 (2.4)	65.5 (4.8)
Deciduous cover (%)	71.1 (4.4)	26.2 (5.2)	69.8 (4.9)	69.5 (4.8)	13.5 (3.3)	34.0 (5.6)	13.3 (3.9)	13.4 (3.0)	16.6 (4.3)
Shrub cover (%)	51.5 (6.2)	38.1 (5.1)	47.6 (7.4)	64.5 (7.7)	46.5 (5.1)	58.9 (6.7)	23.3 (5.3)	17.1 (3.2)	25.0 (4.2)
Canopy composition ^b	A>M>C	H>M>C	A>M>H	A>M>F	F>A>C	A>H>F	H>S>A	H>S>A	H>A>S
Shrub composition ^c	SF>SB>VM	SB>SF>VM	SF>SB>VM	SF>VM>SB	SB>SF>SC	SB>VM \equiv SF	HB>SF>FA	HB>SF>FA	SF \equiv HB>FA

^aActive channel width

^bDominant species in order of abundance based on quantified vegetation composition of trees of stems within 25 m of active channel margins: A, alder; C, cedar; F, fir; H, hemlock; M, maple; S, spruce.

^cDominant species in order of abundance based on quantified vegetation composition of understory shrubs within 20 m of active channel margins: FA, false azalea; HB, huckleberry; SB, salmonberry; SC, stink currant; SF, swordfern; VM, vine maple.

to 9.6 m at mixed sites (Table 1). Discharge during the study varied from a low of $<0.01 \text{ m}^3 \cdot \text{sec}^{-1}$ in the fall to a high of $0.75 \text{ m}^3 \cdot \text{sec}^{-1}$ in the winter. Mean air temperatures during the study ranged from 3 °C in March to 15 °C in July. Mean water temperatures ranged from 4 °C in March to 14 °C in August.

Invertebrate Prey Availability

Overall, Diptera yielded the greatest benthic biomass sampled in the three vegetation types, varying from 27% to 43% of the sample (Table 2). Plecoptera were also abundant, varying from 17% to 49% of the biomass. Ephemeroptera and Trichoptera were also common. Together these taxa represented approximately 90% of the benthic invertebrate biomass collected.

Diptera and Plecoptera were dominant among seasons (Fig. 2). Although absolute estimates of biomass varied somewhat by vegetation type within each season, it was lowest during the winter ($p \leq 0.05$; Fig. 3; Table 3). Neither benthic biomass differences among riparian vegetation types ($p = 0.91$) nor riparian type and season interaction ($p = 0.38$) were statistically significant (Table 4), but benthic invertebrate biomass was negatively related to stream discharge at Camp Creek ($r = -0.83$; $p < 0.01$), Tucua Creek ($r = -0.69$; $p < 0.02$), and NF Ecola Creek ($r = -0.64$; $p < 0.03$). High benthic invertebrate biomass estimates occurred at times of low summer and fall base flows. Conversely, low benthic invertebrate biomass estimates coincided with high winter base flow (Figure 4).

Table 2. Percent composition of benthic invertebrate mass collected in Surber samples in deciduous, conifer, and mixed vegetation types from July 2001 – April 2002.

	Riparian Vegetation Type		
	Deciduous	Conifer	Mixed
Coleoptera	4.2	3.4	3.4
Decapoda	5.3	0.0	2.4
Diptera	35.4	26.9	43.4
Ephemeroptera	13.6	11.1	16.7
Gastropoda	0.5	0.7	2.1
Odonata	0.1	0.1	1.4
Plecoptera	29.0	48.8	17.4
Trichoptera	8.6	7.2	9.0
Other ^a	3.3	1.8	4.2

^aIncludes Hemiptera, unidentifiable invertebrates, and taxa that comprise <1%.

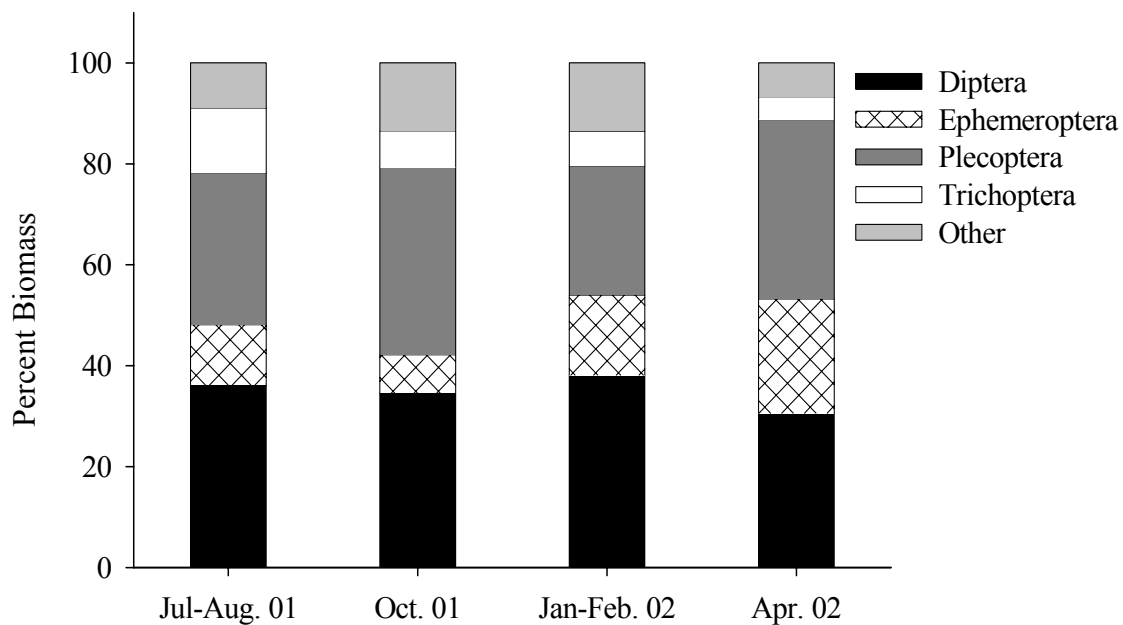


Figure 2. Seasonal changes in percent biomass of benthic invertebrates collected in Surber samples in streams of the Oregon Coast Range from July 2001 to April 2002. Other category consists of Acari, Collembola, Decapoda, Gastropoda, Hemiptera, Neuroptera, Odonata, Oligochaeta, Pelecypoda, and Turbellaria.

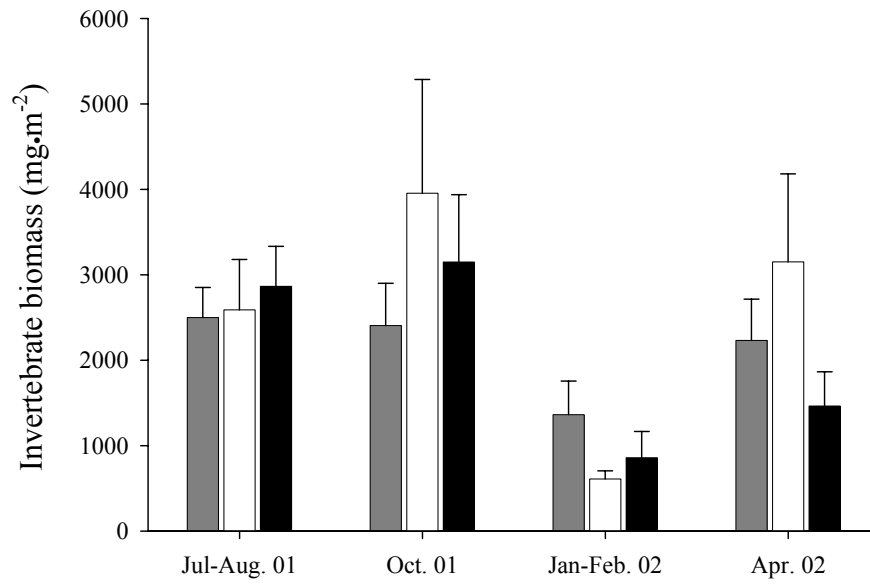


Figure. 3. Seasonal changes in mean biomass of benthic invertebrates in stream sections in deciduous (shaded), conifer (open), and mixed (dark) riparian habitats (n=3/habitat type/season). Error bars represent ± 1 standard error of the mean.

Table 3. Repeated measures analysis of variance and Tukey Kramer multiple means comparison results for the effect of season on invertebrate prey categories (benthic, drift, and allochthonous) and diet of coastal cutthroat trout in stream study sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek of the Oregon Coast Range. Numbers in parentheses indicate ± 1 standard error of the mean.

Response Variables	Summer	Fall	Winter	Spring	F-Statistic	P-Value	Group Comparison ^a
Benthic (dry•mg•m ⁻²)	2651 (273)	3170 (538)	945 (171)	2283 (405)	13.4	< 0.01	Su, F, Sp > W
Drift (dry•mg•m ⁻³ •h ⁻³)	80 (16)	13 (3)	227 (69)	134 (28)	27.6	< 0.01	Su, W, Sp > F
Allochthonous (dry•mg•m ⁻² •d ⁻¹)	124 (10)	64 (9)	15 (2)	21 (3)	18.5	< 0.01	Su > F > W, Sp
Fish diet (dry•mg•fish)	18 (2)	15 (3)	10 (2)	32 (3)	11.0	< 0.02	Sp > Su, F, W

^aTukey Kramer multiple means comparison between seasons: Su, summer; F, fall; W, winter; Sp, spring.

Table 4. Repeated measures analysis of variance and Tukey Kramer multiple means comparison results for the effect of vegetation on invertebrate prey categories (benthic, drift, and allochthonous) and diet of coastal cutthroat trout in stream study sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek of the Oregon Coast Range. Numbers in parentheses indicate ± 1 standard error of the mean.

Response Variables	Deciduous	Conifer	Mixed	F-Statistic	P-Value	Group Comparison ^a
Benthic (dry•mg•m ⁻²)	2125 (219)	2576 (461)	2084 (280)	0.1	0.91	No difference
Drift (dry•mg•m ⁻³ •h ⁻³)	129 (49)	94 (21)	117 (33)	0.01	0.98	No difference
Allochthonous (dry•mg•m ⁻² •d ⁻¹)	64 (8)	45 (6)	61 (7)	5.6	0.04	D, M > C
Fish diet (dry•mg•fish)	21 (2)	20 (2)	16 (2)	0.5	0.63	No difference

^aTukey Kramer multiple means comparison between seasons: D, deciduous; C, conifer; M, mixed.

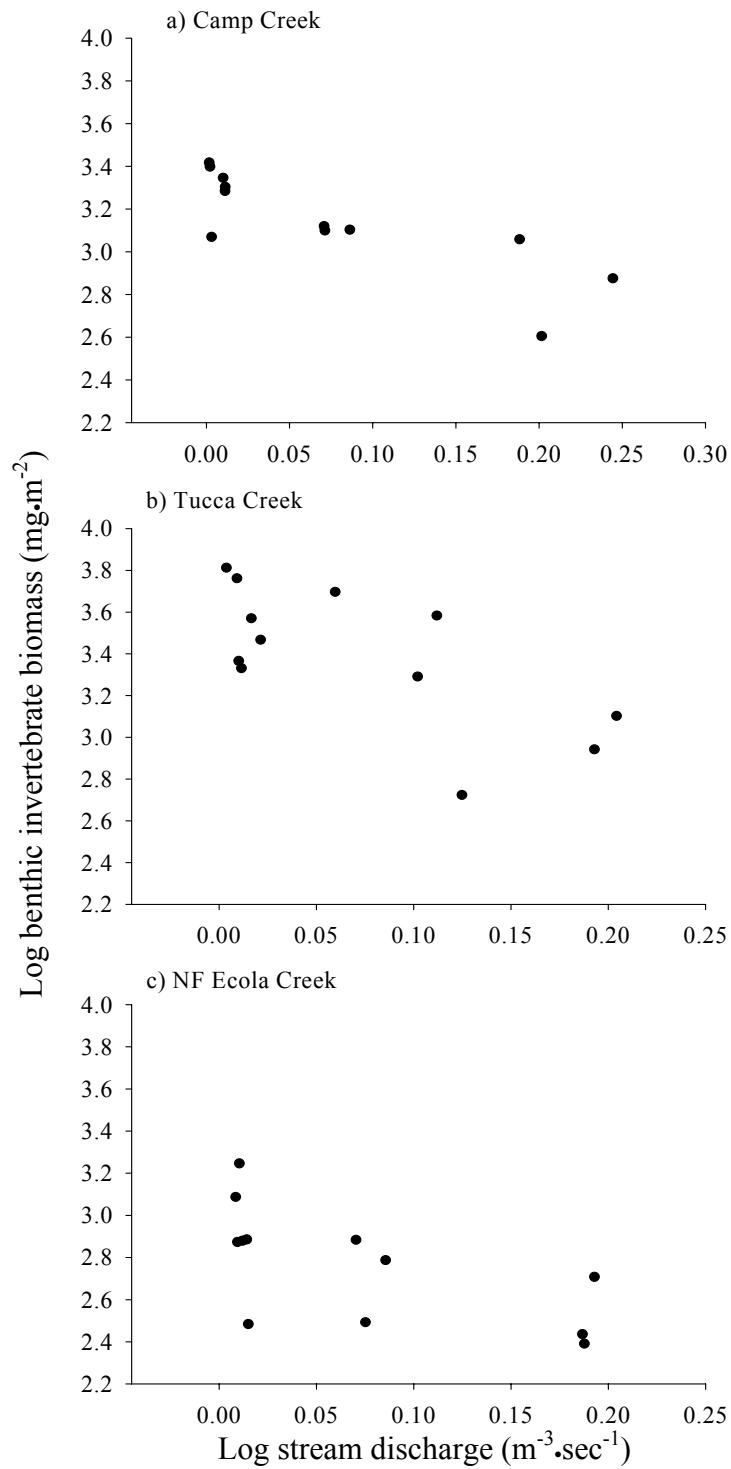


Figure 4. Relationship between benthic invertebrate biomass (dark) and stream discharge (open bar) with Pearson correlation coefficients in (a) Camp Creek ($r = -0.83$; $P < 0.01$), (b) Tucua Creek ($r = -0.69$; $P < 0.02$), and (c) NF Ecola Creek ($r = -0.64$; $P < 0.03$) from July 2001 to April 2002 ($n=3/\text{habitat type/season}$). Error bars represent ± 1 standard error of the mean.

Seasonal differences in total drifting invertebrate biomass were statistically significant ($p \leq 0.05$; Table 3). Aquatic taxa comprised 78%, 66%, 99%, and 91% of drifting invertebrate biomass in summer, fall, winter, and spring, respectively. Aquatic invertebrate biomass drift rate ranged from $9 \text{ mg}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$ in the fall to $215 \text{ mg}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$ in the winter. Ephemeroptera comprised the largest percentage of drifting biomass sampled in each season, contributing about 30% in the summer, fall, winter and 60% in the spring (Fig. 5). The biomass of drifting aquatic organisms in deciduous, conifer, and mixed riparian vegetation types displayed relatively similar patterns for three of the seasons, but in winter drift biomass in conifer sites was less than in deciduous and mixed vegetation sites by a two-fold difference (Fig. 6). The biomass of drifting terrestrial invertebrates ranged from $3 \text{ mg}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$ in the winter to $25 \text{ mg}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$ in the summer. Overall, drifting terrestrial invertebrates in deciduous, conifer, and mixed riparian types declined from summer levels to a low in winter, gradually increasing in spring to levels that were similar to the previous summer. There were no significant differences in drifting invertebrate biomass among riparian vegetation types ($p = 0.98$; Table 4). Total invertebrate drift rate was positively correlated with stream discharge at Camp Creek ($r = 0.71$; $p < 0.01$), Tucua Creek ($r = 0.72$; $p < 0.01$), and North Fork Ecola Creek ($r = 0.44$; $p > 0.15$) (Fig. 7). Annual high drift rate estimates in winter samples were associated with elevated winter base flows, and low drift rate estimates in fall samples were related to annual low base flows (Fig. 7).

Diptera, Trichoptera, Plecoptera, and Coleoptera composed the largest fraction of allochthonous invertebrate biomass in pan traps collected in deciduous, conifer, and

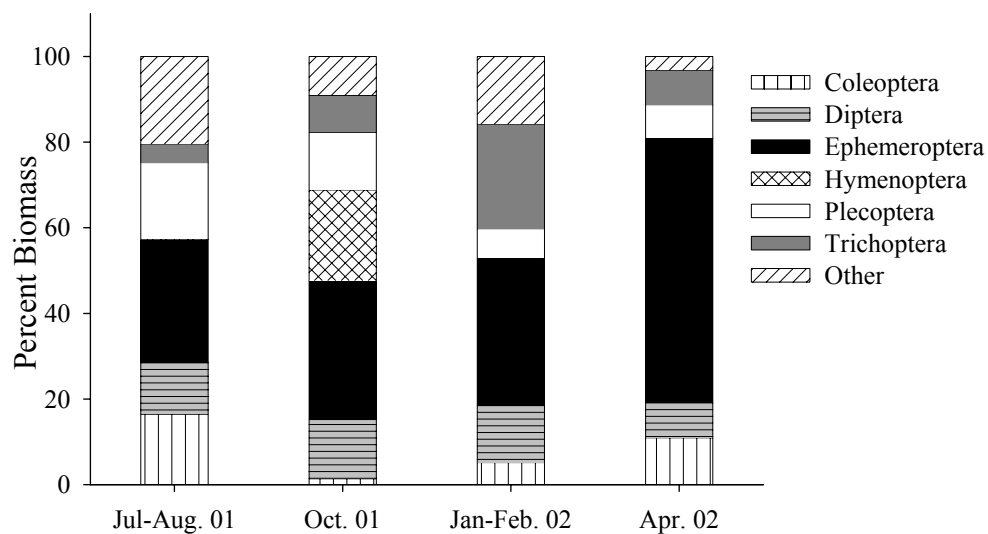


Figure 5. Seasonal changes in percent biomass of drifting invertebrates collected in streams of the Oregon Coast Range from July 2001 to April 2002. Other category consists of Acari, Araneida, Chelothenida, Chilopoda, Collembola, Decapoda, Diplopoda, Gastropoda, Hemiptera, Homoptera, Odonata, Oligochaeta, Pelecypoda, and Psocoptera.

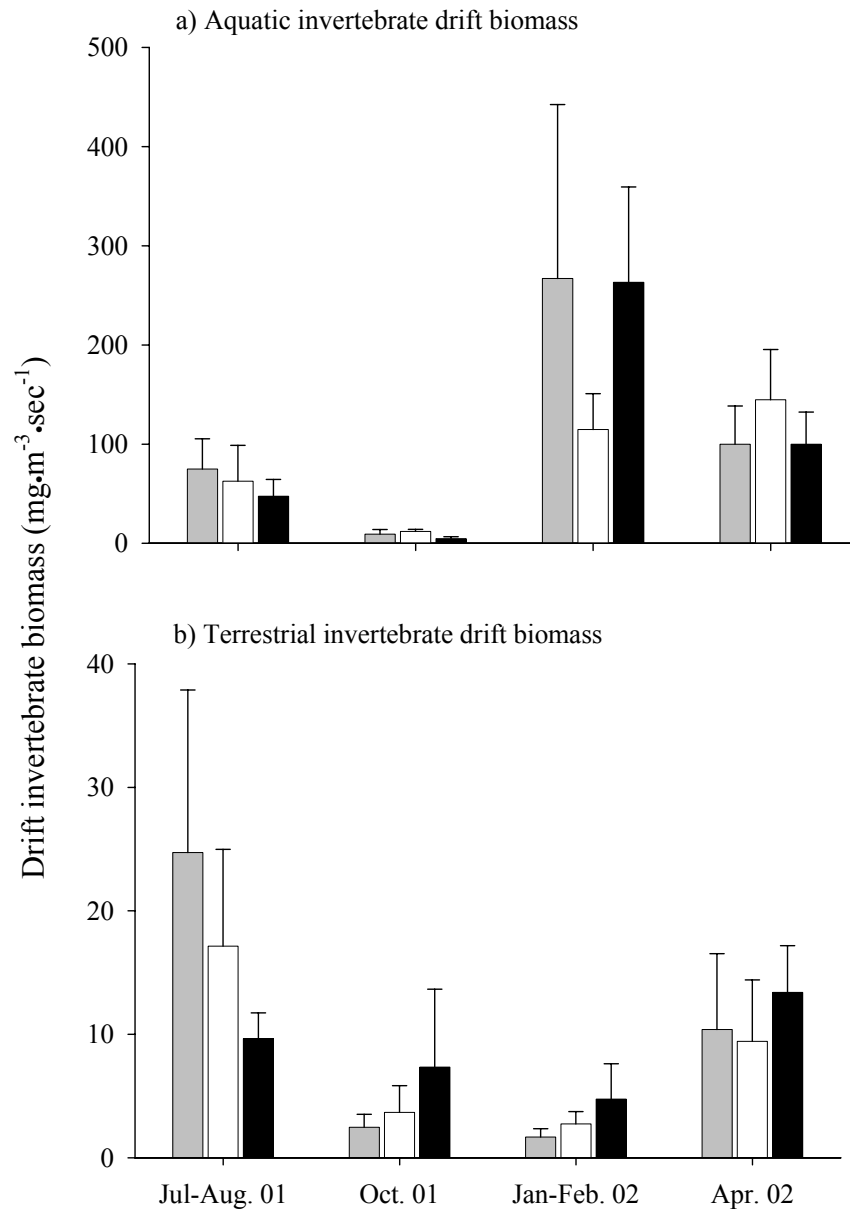


Figure 6. Seasonal changes in mean drifting invertebrate biomass of (a) aquatic invertebrates and (b) terrestrial invertebrates captured in stream sections in deciduous (shaded), conifer (open), and mixed (dark) riparian habitats, averaged across all nine study sections ($n=3$ /vegetation type/season). Error bars represent ± 1 standard error of the mean.

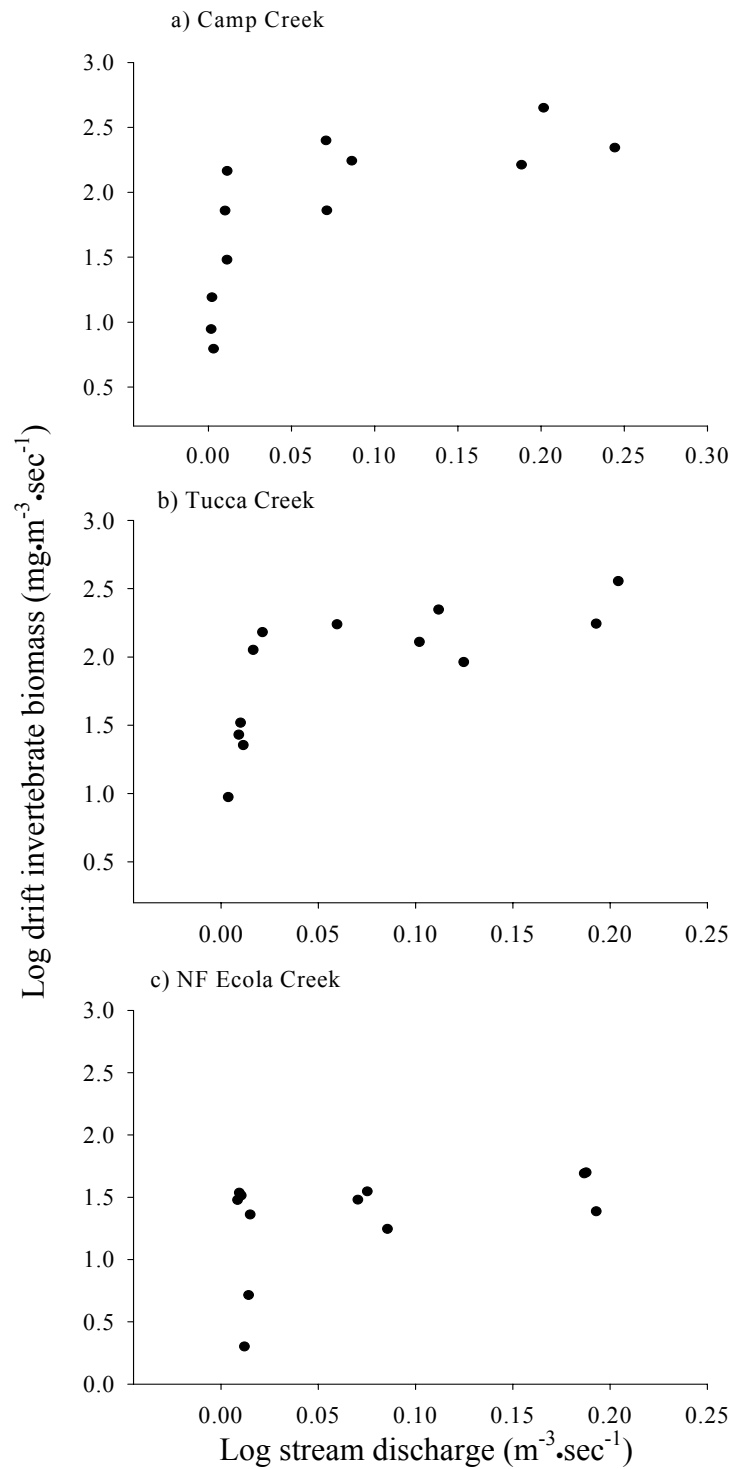


Figure 7. Relationship between drifting invertebrate biomass (dark) and stream discharge (open bar) with associated Pearson correlation coefficients in (a) Camp Creek ($r = 0.71$; $P < 0.01$), (b) Tucua Creek ($r = 0.72$; $P < 0.01$), and (c) NF Ecola Creek ($r = 0.44$; $P < 0.06$) from July 2001 to April 2002 ($n=3$ /vegetation type/season). Error bars represent ± 1 standard error of the mean.

mixed vegetation types (Table 5). The mean mass of invertebrates captured in pan traps combined was estimated at $56 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Diptera yielded the largest biomass of invertebrates captured in pan traps, contributing $18.4 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Diptera of aquatic origin contributed $6.9 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ compared to $8.3 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ for terrestrially derived Diptera. Diptera of unknown origin, primarily Empididae, accounted for $3.4 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Aquatic emergent adult insects consisting primarily of Ephemeroptera, Diptera, Plecoptera, and Trichoptera comprised about half of the total insects captured in pan traps during all seasons. Diptera was the most prevalent taxon in all seasons comprising approximately 30% of the biomass in summer, fall, and spring, and over 80% of the biomass in the winter (Fig. 8). Trichoptera contributed substantially to the invertebrate biomass collected in the summer and fall, and Coleoptera were common in the spring.

Differences in total allochthonous invertebrate biomass collected in pan traps among seasons were statistically significant ($p < 0.05$; Table 3), and biomass was greatest during summer and fall (Fig. 9). Biomass of aquatic and terrestrial insects from pan traps declined steadily from a peak in summer to lows in winter and spring (Fig. 9). Total invertebrate biomass collected in pan traps was positively correlated with air temperature in Camp Creek ($r = 0.85$; $p < 0.01$), Tucua Creek ($r = 0.80$; $p < 0.01$) and North Fork Ecola Creek ($r = 0.55$; $p < 0.06$) (Fig. 10). Differences in total invertebrate biomass in pan traps between the conifer riparian sites ($44.9 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) and deciduous and mixed riparian sites (64.3 and $60.9 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, respectively) were statistically significant ($p \leq 0.05$; Table 4). The amount of variation in invertebrate

Table 5. Percent composition of invertebrate mass captured in pan traps, collected from deciduous, conifer, and mixed riparian types from July 2001 – April 2002.

	Riparian Vegetation Type		
	Deciduous	Conifer	Mixed
Aquatic			
Coleoptera	0.3	1.2	0.0
Diptera	11.9	13.8	12.1
Ephemeroptera	5.9	4.8	5.4
Hemiptera	2.5	0.0	1.0
Odonata	8.3	0.0	0.0
Plecoptera	7.3	9.3	12.0
Trichoptera	22.4	16.0	15.2
Terrestrial			
Araneida	2.1	2.1	2.5
Coleoptera	8.2	6.3	6.7
Diptera	16.1	17.8	13.3
Homoptera	1.9	0.9	1.5
Hymenoptera	1.1	9.4	5.6
Lepidoptera	3.9	7.2	5.9
Orthoptera	1.0	4.0	0.7
^a Other	7.1	7.2	18.1

^aIncludes unidentifiable invertebrates and taxa that comprise <1%.

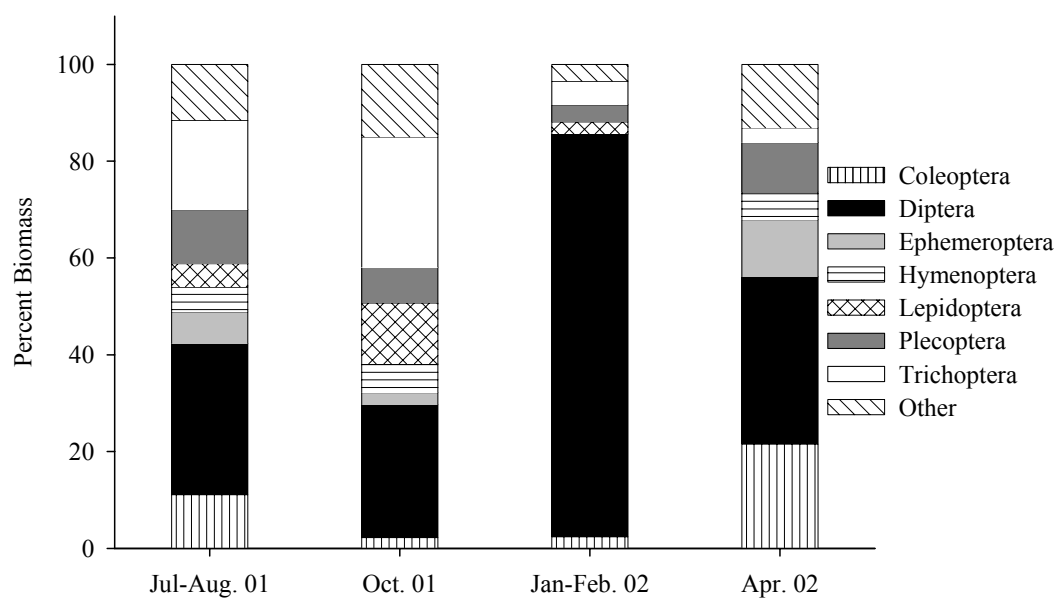


Figure 8. Seasonal changes in percent biomass of invertebrates collected in allochthonous pan trap in streams of the Oregon Coast Range from July 2001 to April 2002. Other consists of Araneida, Collembola, Diplopoda, Hemiptera, Homoptera, Neuroptera, Odonata, Opiliones, Psocoptera, Thysanura.

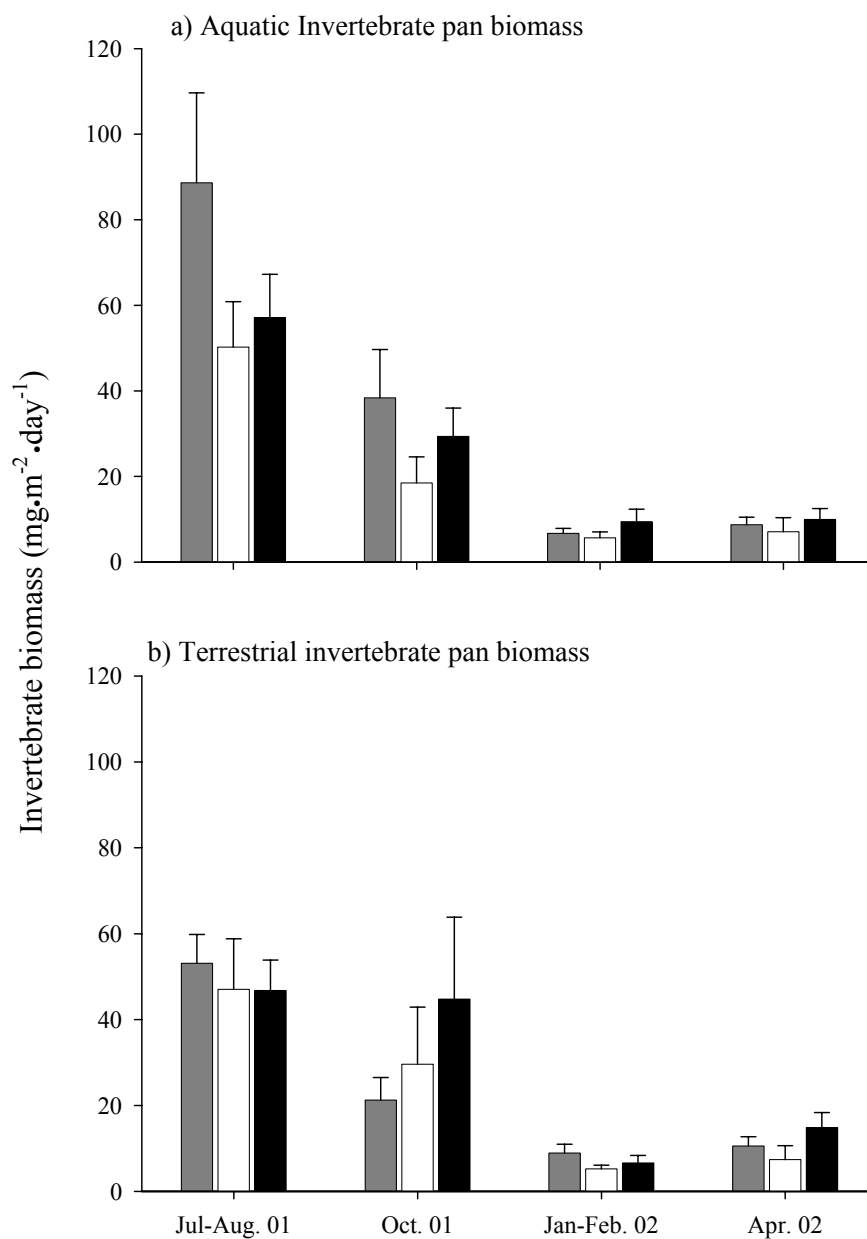


Figure 9. Seasonal changes in mean biomass of (a) aquatic and (b) terrestrial invertebrates captured in allochthonous pan-traps in stream sections in deciduous (shaded), conifer (open), and mixed (dark) riparian habitats (n=3/vegetation type/season). Error bars represent ± 1 standard error of the mean.

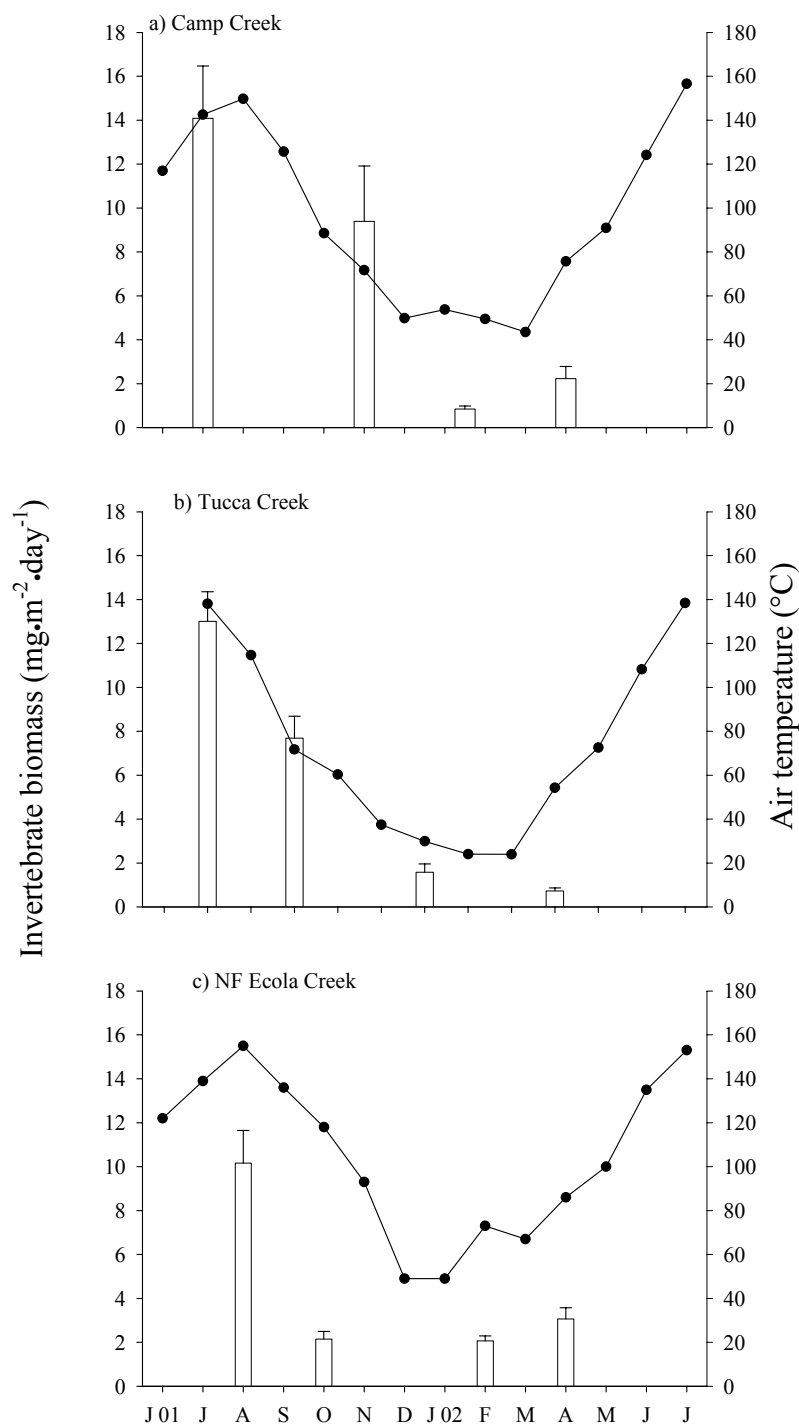


Figure 10. Relationship between invertebrate biomass captured in pan traps (open bars) and air temperature from July 2001 to April 2002. Pearson correlation coefficients are as follows: (a) Camp Creek ($r = 0.85$; $P < 0.01$), (b) Tucua Creek ($r = 0.80$; $P < 0.01$), and (c) NF Ecola Creek ($r = 0.55$; $P < 0.06$) ($n=3/\text{vegetation type/season}$). Error bars represent ± 1 standard error of the mean.

biomass that was explained by the riparian type and season interaction was not statistically significant ($p = 0.74$).

Coastal cutthroat trout diet

Coastal cutthroat trout ingested a diverse variety of prey that included 70 identified families in 27 orders from a total of 667 fish sampled. Aquatic invertebrates were the most common (61% of families) taxa collected. The mean mass of prey ingested per fish at all sites and seasons combined was $19.1 \text{ mg}\cdot\text{fish}^{-1}$. Invertebrates of aquatic origin comprised 56% of total identifiable prey mass ingested. Common prey items ingested included Ephemeroptera, Trichoptera, Plecoptera, and Diptera. Terrestrially derived invertebrates composed only 35% of the diet by mass. Coleoptera, Orthoptera, Araneida, and Homoptera were the dominant terrestrial taxa in the diet (Table 6). The proportion of Plecoptera was relatively constant among seasons, but the contribution of other taxa varied among seasons (Fig. 11).

Seasonal differences in biomass of invertebrates ingested by coastal cutthroat trout were statistically significant ($p \leq 0.05$; Table 3). Ingested prey mass of aquatic and terrestrial origin was similar during the summer and fall sampling periods (Fig. 12). In winter there was little change in mass of aquatic insects ingested, but mass of terrestrial insects declined to a low of $<1 \text{ mg}\cdot\text{fish}^{-1}$. These values suggest that total ingested mass declined to almost half of summer and fall levels. During the spring sampling period, ingested mass of invertebrates of terrestrial origin was similar to

Table 6. Percent composition of invertebrate mass ingested by coastal cutthroat trout in deciduous, conifer, and mixed riparian types.

	Riparian Forest Type		
	Deciduous	Conifer	Mixed
Aquatic			
Coleoptera	0.9	0.4	2.1
Decapoda	3.0	3.5	1.0
Diptera	9.0	6.0	6.1
Ephemeroptera	13.7	17.9	27.3
Hemiptera	0.4	0.5	2.0
Plecoptera	15.1	10.6	9.9
Trichoptera	15.3	13.1	13.0
Terrestrial			
Araneida	5.1	6.8	2.5
Chilopoda	2.2	0.2	0.6
Coleoptera	8.3	6.5	8.6
Diplopoda	2.3	4.0	2.0
Diptera	5.1	1.0	1.1
Gastropoda	0.0	2.9	0.0
Hemiptera	0.4	0.4	0.4
Homoptera	5.7	3.6	2.7
Hymenoptera	1.4	0.6	2.2
Isopoda	0.2	0.4	0.7
Lepidoptera	1.3	2.0	0.9
Orthoptera	6.0	1.6	11.9
Unknown			
Oligochaeta	1.1	11.7	0.1
Other ^a	3.5	6.3	4.9

^aIncludes Isoptera, Neuroptera, and Thysanura and unidentifiable invertebrates and taxa that comprise <1%.

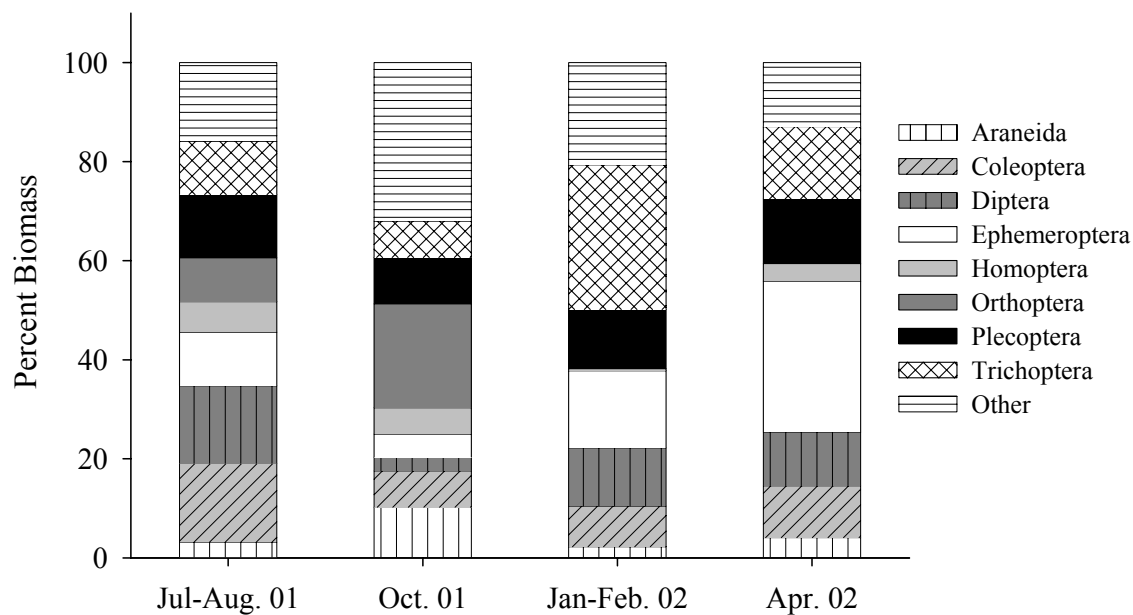


Figure 11. Seasonal changes in percent biomass of invertebrates ingested by coastal cutthroat trout in streams of the Oregon Coast Range from July 2001 to April 2002. Other consists of Acari, Collembola, Decapoda, Gastropoda, Hemiptera, Neuroptera, Odonata, Oligochaetae, Pelecypoda, Turbellaria.

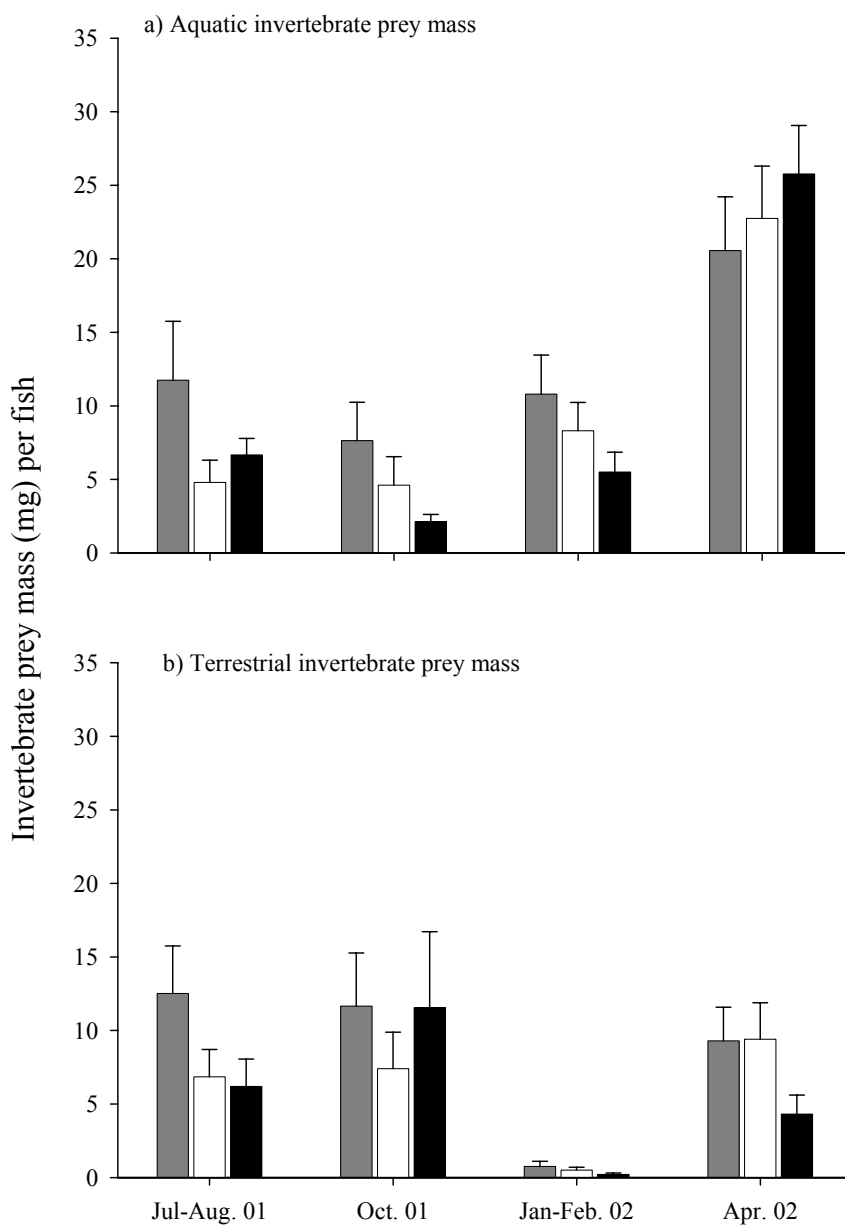


Figure 12. Seasonal changes in mean mass of (a) aquatic and (b) terrestrial invertebrate prey ingested by 80-220 mm total length coastal cutthroat trout in stream study sections in deciduous (shaded), conifer (open), and mixed (dark) riparian habitats ($n=3$ /vegetation type/season). Error bars represent ± 1 standard error of the mean.

summer-fall levels, and aquatic invertebrates prey mass reached a maximum that was almost twice previously observed levels. Differences in invertebrate mass ingested were not statistically significant among riparian types ($p = 0.63$; Table 4), and variation in consumption explained by riparian type and season interaction was not statistically significant ($p = 0.74$).

Aquatic prey mass was greater than terrestrial prey mass in the winter and spring ($p < 0.07$). Aquatic prey mass accounted for 47%, 31%, 94%, and 74% of the identifiable organisms in the diet in summer, fall, winter, and spring, respectively. In general, terrestrial prey mass was more prevalent in cutthroat trout diets in the fall, but in winter and spring the biomass of aquatic taxa was greatest.

Coastal cutthroat trout Relative condition (K_n)

Differences in coastal cutthroat trout condition were statistically significant among seasons ($p \leq 0.05$). Fish condition was highest during the summer sampling period and lowest in the following spring (Fig. 13). Differences in coastal cutthroat trout condition were not statistically significant among riparian types ($p = 0.87$), and the riparian type by season interaction did not explain a statistically significant amount of variation in condition ($p = 0.71$). Mean fish condition was greater in Camp Creek than Tucca and North Fork Ecola Creek, and differences were statistically significant ($p \leq 0.05$) (Fig. 14).

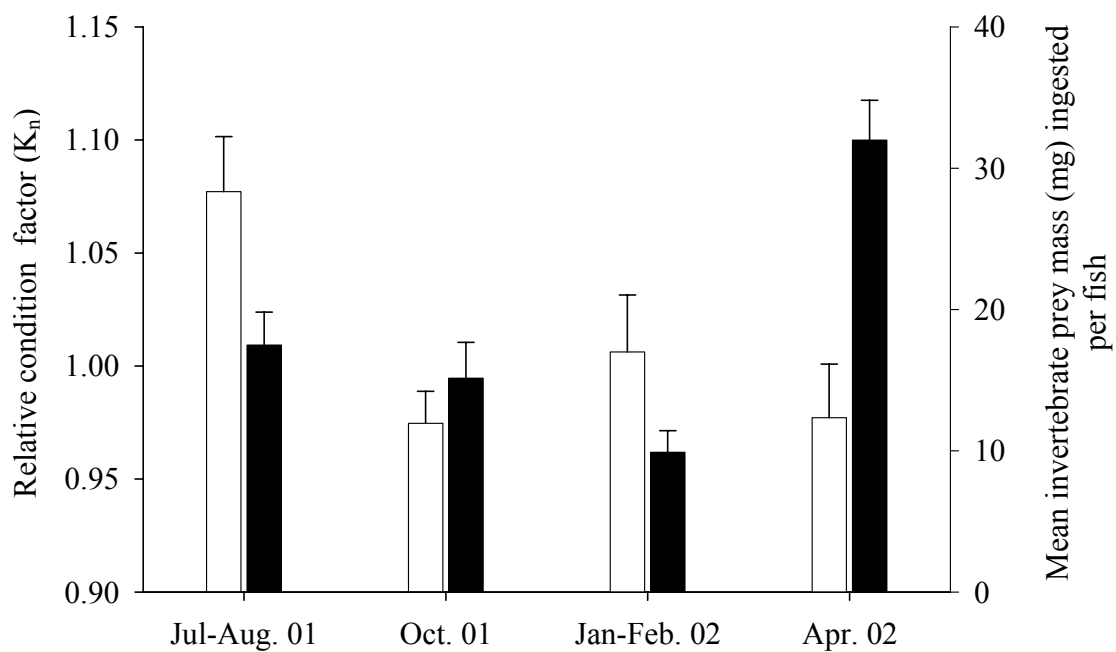


Figure 13. Seasonal changes in mean condition (open) of ≥ 80 mm total length coastal cutthroat trout and total invertebrate prey mass (dark) ingested ($n=3$). Error bars represent ± 1 standard error of the mean.

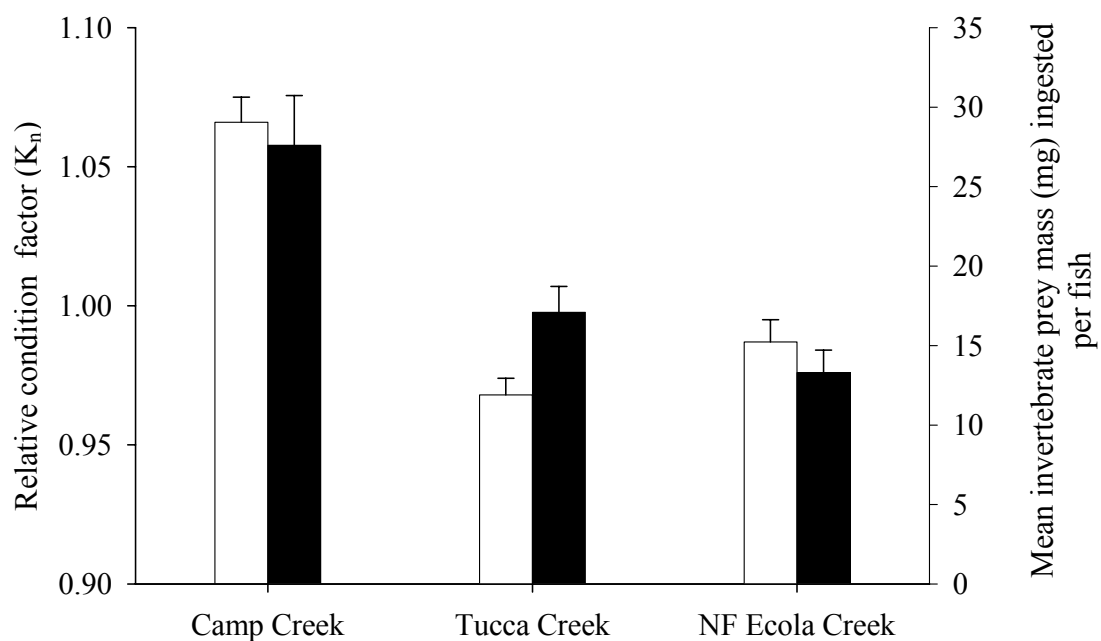


Figure 14. Comparison of mean condition (open) and total prey mass (dark) ingested of ≥ 80 mm total length coastal cutthroat trout in Camp Creek, Tucca Creek, and North Fork Ecola Creek for all vegetation types and seasons combined ($n=3$). Error bars represent ± 1 standard error of the mean.

CHAPTER 4: DISCUSSION

This is a unique attempt to examine the annual invertebrate contribution of riparian plant communities of forested systems to an aquatic food web. Allochthonous invertebrate biomass input was greater in stream sections dominated by deciduous and mixed riparian vegetation types than conifer. Also, patterns of invertebrate prey availability and diet and condition of coastal cutthroat trout were highly variable among seasons in the three streams we sampled. Diet of coastal cutthroat trout was influenced by but not dependent on, distinct temporal patterns of availability of aquatic and terrestrial invertebrates. Furthermore, seasonal changes in coastal cutthroat trout condition were related to prey mass ingested, apparently the result of feeding from the previous season.

Coastal cutthroat trout ingested a wide array of aquatic and terrestrial invertebrates in the streams in the Oregon Coast Range. Invertebrates of aquatic and terrestrial origin comprised approximately 56% and 35% of the identifiable organisms on an annual basis, respectively. Ephemeroptera, Trichoptera, Plecoptera, and Diptera contributed the greatest aquatic mass to the diet of coastal cutthroat trout. Coleoptera, Orthoptera, Araneida, and Homoptera were the most important terrestrial prey items in terms of mass. Our mean estimate $19.1 \text{ mg}\cdot\text{fish}^{-1}$ of prey ingested was higher than estimates of 9.0 and $12.1 \text{ mg}\cdot\text{fish}^{-1}$ reported from southeastern Alaska (Wipfli 1997; Allan et al. 2003), but they were comparable to annual estimates in northern Japan after converted to equivalent units ($29.9 \text{ mg}\cdot\text{fish}^{-1}$ in forest reaches and $10.4 \text{ mg}\cdot\text{fish}^{-1}$ in grassland reaches) (Kawaguchi and Nakano 2001).

Coastal cutthroat trout displayed opportunistic feeding patterns that were related to seasonal changes in allochthonous prey availability. Terrestrial prey organisms contributed substantially to the diet of coastal cutthroat trout in the summer, fall, and spring but were negligible in the winter ($< 1 \text{ mg}\cdot\text{fish}^{-1}$) (Fig. 12). Input of terrestrial invertebrate biomass to streams coincided with observed feeding patterns in the summer and fall (Fig. 9). It has been argued that the prevalence of terrestrial organisms in the diet of salmonids may be related to seasonally varying availability of terrestrial organisms and low benthic macroinvertebrate availability following adult emergence in the summer, fall, and spring (Hynes 1970; Cloe and Garman 1996; Wipfli 1997). This pattern did not hold in our study. Both aquatic adult emergence (Fig. 9) and benthic invertebrate biomass was highest during summer and fall (Fig. 3), but terrestrial invertebrates were more intensely exploited than aquatic invertebrates by coastal cutthroat trout during this period.

Past studies suggest that in streams where salmonids are present, some benthic invertebrate taxa may avoid predation by reducing drift during the day (Waters 1972; Miyasaka and Nakano 2001). Larger aquatic invertebrates preferred by salmonids are often nocturnal and less available (Allan 1978). In contrast, terrestrial prey biomass enters streams, occurs in the drift, and is consumed by salmonids generally during the day more than night (Edwards and Huryn 1995; Nakano et al. 1999). Because terrestrial invertebrates are generally larger than aquatic invertebrates and more conspicuous in the drift during the day (Wilzbach et al. 1986; Edwards and Huryn 1996; Nakano et al. 1999), they represent a readily available prey subsidy to foraging

coastal cutthroat trout during seasons of high availability. In this study, high terrestrial prey mass ingested corresponded to high allochthonous input of terrestrial invertebrate biomass during the summer and fall, but surprisingly we observed relatively low levels of terrestrial invertebrate mass in the drift. Together these findings suggest intensive exploitation of the terrestrial prey during the summer and fall.

During the spring, terrestrial invertebrate biomass input was lower in the spring than the summer and fall (Fig. 9), but consumption rates of terrestrial invertebrate prey mass were similar (Fig. 12). Although terrestrial invertebrate biomass input was lower in the spring than summer and fall (Fig. 9), the availability in the drift was similar (Fig. 6). Periodic rainfall events occurring through the spring may have increased terrestrial invertebrate availability in the drift to coastal cutthroat trout. Changes in discharge and wetted perimeter can also influence inputs of wingless insects (O'Hop and Wallace 1983; Edwards and Huryn 1995). Ingestion of terrestrial invertebrates can be substantial for short periods of time following events such as wind and rainstorms (McCormack 1962). For example, wingless terrestrial invertebrates composed 42% of the terrestrial prey mass ingested by coastal cutthroat trout but only 12% of the terrestrial prey biomass collected in allochthonous pan traps. Furthermore, pan traps may have been less efficient in sequestering wingless terrestrial prey during the spring (Wipfli 1997).

Although terrestrial invertebrate biomass input estimates were similar in winter and spring (Fig. 9), ingestion of terrestrial invertebrates was significantly lower in winter (Fig. 12). Several possible explanations may account for this apparent

discrepancy. First, pan traps in the winter may have attracted certain taxa, like winged Diptera disproportionately (Southwood 1961; Edwards and Huryn 1995; Wipfli 1997). For example, winged Diptera, consisting almost entirely of Mycetophilidae, accounted for approximately 90% of the estimated terrestrial invertebrate biomass input in the winter but comprised less than 0.3% of the terrestrial prey mass ingested. In the spring the composition of terrestrial prey collected in allochthonous pan trap samples was more diverse (70% of terrestrial biomass consisted of Araneida, Coleoptera, Collembola, Homoptera, Hymenoptera, and Orthoptera) and reflective of terrestrial prey consumption. After Diptera were removed from pan trap samples, estimates of terrestrial invertebrate biomass were 1.2 and $7.1 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ during winter and spring, respectively. Because the input of invertebrates from allochthonous sources is strongly influenced by overhanging vegetation (Mundie 1969; Cadwallader et al. 1980), it is also possible that randomly placed pan traps in the stream channel may have underestimated allochthonous input from this source.

During the winter, the availability of drifting aquatic invertebrates was much greater than the summer and fall, but differences in aquatic invertebrate prey mass ingested were not statistically significant among summer, fall, and winter. Our empirical measure of low winter feeding rates in coastal cutthroat trout follow results of other studies that examined several factors likely influencing winter feeding. First, suspended inorganic and organic particles associated with chronic spates occurring through the winter may have decreased foraging efficiency of coastal cutthroat trout. Past studies have shown that trout exposed to increasing levels of suspended

sediments experienced significant reductions in their ability to detect prey (Noggle 1978; Barrett et al. 1992; O'Brien and Showalter 1993), and, as a result, feeding rates (Sigler et al. 1984; Redding et al. 1987; Barrett et al. 1992) and foraging behavior decline (Vinyard and O'Brien 1976; Berg and Northcoate 1985).

Second, current velocity influences foraging success of stream-dwelling salmonids (Godin and Rangle 1989; O'Brien and Showalter 1993). For example, reaction distance and foraging rates for drifting invertebrates decrease with increasing current velocity (Grant and Noakes 1986; Godin and Rangle 1989; Hughes and Dill 1990). Prey encounter rates of drift feeding Arctic grayling (36-41 cm) plateaued at water velocities from 0.30 to 0.50 m.s⁻¹ and then declined as velocity continued to increase (Hughes and Dill 1990; O'Brien and Showalter 1993). Fish sampled in the present study were much smaller (8-23 cm) and would be expected to hold foraging positions in lower water velocity. Mean current velocities measured increased in riffle habitat to 0.52 m.s⁻¹ in winter, and it is likely that high current velocity negatively affected reaction rate of the small trout (80-230 mm). Indeed, Heggenes et al. (1991) demonstrated that coastal cutthroat trout generally avoided habitat with water velocities ≥ 0.20 m.s⁻¹, and avoidance was highest at water velocities ≥ 40 m.s⁻¹. Conversely, during the summer and fall, coastal cutthroat trout may have been more efficient at detecting and capturing prey by holding optimal foraging positions during periods of low velocity and high visibility.

Third, it is likely that low winter water temperature set a physiological limit to the rate of consumption regardless of prey availability. In laboratory experiments the rate

of digestion for salmonids declined at low water temperatures (1 – 5 °C) and increased at intermediate temperatures (13 – 17 °C) (Brett and Higgs 1970; Dwyer and Kramer 1975). For example, winter food intake in Convict Creek, California was less than half of that observed in the summer and fall, despite more abundant prey during some winter months (Reimers 1963). Average water temperature at our sites ranged from 5 – 6 °C in winter, and low metabolic levels at low water temperatures likely suppressed coastal cutthroat trout feeding.

Lastly, feeding rates of coastal cutthroat trout during the winter may have decreased with the shortened photoperiod. In the Oregon Coast Range, daylight hours range from a peak of 15 h during the summer to a low of 8 h during the winter. Although we did not examine diel-feeding patterns in this study, numerous studies have indicated that salmonids do not generally feed at night (Bisson 1978, Allan 1981, Angradi and Griffith 1990). Young et al. (1997) demonstrated that Colorado cutthroat trout foraged primarily during the day in the summer and speculated that low light intensities prevented trout from exploiting the nocturnal increase in drifting invertebrates. In Oregon Coast streams shortened winter foraging periods would have likely contributed to reduced consumption levels for coastal cutthroat.

During the spring, foraging conditions appeared to improve, and coastal cutthroat trout appeared to feed in relation to aquatic prey availability in the drift (Fig.6). Declines in stream discharge and increases in water temperature and photoperiod were noted during this period. These factors may have acted synergistically to increase metabolic activity and stimulate intensive feeding as trout emerged from annual lows

of prey consumption during the winter, and mass of aquatic invertebrate prey ingested reached a maximum that was nearly a three-fold increase of previously observed levels (Fig. 12).

It has been argued that food limitation sets an upper limit on growth and productivity of stream salmonids (Cada et al. 1987; Filbert and Hawkins 1995). Coastal cutthroat trout inhabiting the three Oregon Coast Range streams we sampled exhibited seasonal changes in fish condition that appeared to reflect the level of prey consumption. In contrast, to coastal cutthroat trout in a small Washington stream where fish condition peaked in the winter followed by declining rates through the summer (Martin 1984), trout at our sites had significantly higher condition in summer and declined through the following seasons (Fig. 13). The highest levels of ingested prey mass were observed in the spring samples, and may partially explain improved fish condition during the summer. Increased fish condition in the summer may be related to intensive feeding through the spring, but other factors such as increased energy demands for gonad development, gamete production, and spawning migrations may also have influenced condition factors during the spring. Likewise, the relative paucity of invertebrate prey in the drift during the summer and fall may partially explain observed declines in fish condition during the fall and winter. Although invertebrate availability was high in winter, high discharge may have reduced foraging efficiency and associated fish condition in the spring. In a comparison of fish condition across sites, total prey mass ingested was significantly highest in Camp Creek, and highest condition was also recorded in Camp Creek (Fig. 14). These

findings lend support to the hypothesis that condition factors directly reflect foraging levels.

Wet winters, moderately wet springs, and dry summer and fall seasons characterize seasonal precipitation patterns of the Oregon Coast Range. As a result, episodic high flow events regularly occur through the winter and decline in spring. Correspondingly, invertebrate biomass at all sites displayed an annual low during the winter (Fig. 2), varying inversely with seasonal changes in stream discharge.

Seasonal variation of drifting invertebrate biomass was the inverse of benthic patterns. Drifting invertebrate biomass was positively associated with stream discharge, and estimates of invertebrate biomass in the drift closely tracked seasonal discharge patterns. It is probable that as sheer stress and bedload movement increases during high flow, many invertebrates become dislodged from the streambed (Scrimgeour and Winterbourn 1989; Angradi 1997) and either enter the drift (Brittain and Eikeland 1988) or are crushed (Scrimgeour and Winterbourn 1989). Paustian and Beschta (1979) showed that peak suspended sediment concentration in an Oregon stream occurs slightly before peak discharge. Other studies have shown that maximum organic seston concentrations occurred at or near peak discharge (Bilby and Likens 1979; Gurtz et al. 1980). O'Hop and Wallace (1983) demonstrated that maximum invertebrate drift coincided with peaks of fine and coarse detritus transport. As discharge increases, easily dislodged detritus with accompanying organisms are quickly entrained (O'Hop and Wallace 1983).

The rapid recovery of the benthic community in the spring from lows in the winter suggests that macroinvertebrates are resilient to high flow disturbance in streams of the Oregon Coast Range. Although benthic invertebrate biomass was reduced by 70% from fall to winter, we recorded a 59% increase from winter to spring. One possible explanation for the rapid recovery of the benthic community is that invertebrates take advantage (or use) refugia in high flows. Retentive structures such as instream woody debris and boulders offer structural stability to stream channels that only become dislodged under extreme flood events (Speaker et. al 1984; Gregory et. al 1991). Although bedrock outcrops in the stream channel are common, sites in our study are characterized by riffles with substantial alluvium that generally exceeds >30 cm in depth. Following disturbances that scour surficial deposits and associated organisms (Williams and Hynes 1974; Palmer et al. 1992; Griffith and Perry 1993), this deep alluvium serves as a potential source for recolonization that likely supports rapid recovery of benthic fauna after winter spates (Cushing and Gaines, 1989, Angradi 1997).

Invertebrate input from allochthonous sources also exhibited distinct patterns of temporal availability. Correlations indicated that invertebrate biomass input was positively associated with air temperature; peak input occurred in the summer, and lows in winter and spring. Nakano and Murakami (2001) showed that terrestrial invertebrate input to a small, forested stream in northern Japan closely tracked ambient air temperature and leaf phenology. Mean estimates of allochthonous arthropod inputs to a stream in southern England ranged from 51 to 183 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (April – October),

with peaks during late May-early June and August-September (Mason and MacDonald 1982). Cloe and Garman (1996) reported similar trends in arthropod input estimates from spring through winter (3 to 223 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$), with summer representing the period of greatest allochthonous invertebrate input and winter the lowest. Mean allochthonous invertebrate input to a small, forested stream in northern Japan were 7 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in spring, 87 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in summer, 15 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in fall, and 0.5 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in winter (Kawaguchi and Nakano 2001). In this study, mean seasonal inputs of terrestrial insects ranged from 7 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ during the winter to 49 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ during the summer. Though summer peak input was lowest in Oregon Coast streams, winter input averaged greater than comparable studies in other regions. These comparisons, all based on pan traps, suggest that the terrestrial invertebrate subsidy can differ by at least a factor of two, depending on season and region.

In this study differences in total invertebrate biomass between the conifer riparian sites (45 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) and deciduous and mixed riparian sites (64 and 61 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, respectively) were statistically significant. Deciduous and mixed sites in this study contained a denser understory (Table 1). This understory community likely supported a more diverse and productive allochthonous invertebrate community. Though input of terrestrial invertebrates sometimes differs considerably among deciduous tree species (Mason and MacDonald 1982), a greater abundance of invertebrates are generally associated with deciduous trees than conifers (Southwood 1961). Furthermore, deciduous trees support higher invertebrate mass per stem than conifers (Allan et al. 2003). Shrub cover was lowest in the conifer sites at the 3 streams in this

study (Table 1). Less diverse and less dense understories of 50 to >200-year-old conifer stands like those in this study may also contribute lower invertebrate biomass and densities.

Stream input of invertebrates from allochthonous sources is also affected by overhanging vegetation (Mundie 1969 and Cadwallader et al. 1980). In this study, salmonberry and vine maple were found in higher densities and generally closer to stream margins in deciduous and mixed sites than conifer. Because the streams were small (5-9 m), it is likely that overhanging vegetation strongly influenced invertebrate inputs.

Differences in prey availability (benthic, drift, and allochthonous sources) and fish diet were compared among deciduous, conifer, and mixed vegetation types. Of these comparisons, only allochthonous prey availability varied among vegetation types. None of the instream responses (benthic and drift availability and fish diet) exhibited statistical differences by vegetation type. Although identifying the causes for these between terrestrial and aquatic response differences is beyond the scope of this study, it is apparent that the complex nature of aquatic food webs could not be captured in the simplistic design of this study. Unlike terrestrial environments, streams are unidirectional systems, and organic matter is transferred from upstream habitats to downstream habitats (Vannote et al. 1980). Although we did not directly measure organic transport and retention capacity, upstream influences may have affected instream responses. Furthermore, a statistical difference in allochthonous

invertebrate inputs among vegetation types suggest that instream responses were likely operating at a greater scale.

Estimates of allochthonous invertebrate input suggest that the terrestrial environment provides a substantial subsidy for the energy needs of coastal cutthroat trout during the summer and fall. During summer and fall combined, we observed a mean of 22, 13, and 14 $\text{mg}\cdot\text{fish}^{-1}$ of prey ingested in deciduous, conifer, and mixed vegetation types, respectively. Because gut clearance times are approximately ≈ 24 h at between 8 °C and 12 °C, this is an approximate estimate of daily feeding rate (Elliot and Persson 1978). Assuming coastal cutthroat trout feed at a sustained rate of 20 $\text{mg}\cdot\text{day}^{-1}$ (Elliot 1975; Dunbrack 1988), allochthonous inputs alone (64 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in deciduous, 45 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in conifer, and 61 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in mixed) could support approximately 2-3 coastal cutthroat trout per square meter of stream over the summer and fall. Because aquatic prey in the drift is low during the summer and fall and metabolic demands are high, the terrestrial invertebrate prey subsidy may be potentially substantial.

CHAPTER 5: CONCLUSION

Limited information exists on the life history of isolated populations of potomodromous coastal cutthroat trout (Trotter 1989, Hendricks 2001). By examining the diet of coastal cutthroat trout throughout the year, we were able to document seasonal patterns in feeding and condition in relation to prey availability. These results suggest seasonal patterns of invertebrate prey availability and diet of coastal cutthroat trout in streams of the Oregon Coast Range interact in complex ways with environmental factors and biotic conditions. In the highly variable environment of the Oregon Coast Range, discharge appeared to be an influential factor regulating the biomass of aquatic insects in the benthos and drift. Also, these results suggest that riparian vegetation type can influence the biomass of arthropods entering the stream. We showed that allochthonous invertebrate inputs were greater in deciduous and mixed vegetation types than conifer and differences were statistically different. Based on the evidence that coastal cutthroat trout receive an important percentage of their food supply from allochthonous inputs and that this subsidy varies with the type of riparian vegetation, riparian management should note the importance of deciduous and mixed vegetation to this allochthonous subsidy. The data suggest systematic removal of deciduous vegetation in riparian zones to promote conifer growth and retention is likely to influence food resources of coastal cutthroat trout and may have unintended consequences on the food resources of coastal cutthroat trout and the productivity of aquatic food webs in the Pacific Northwest.

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APPENDICES

Table A.1. Seasonal changes in aquatic invertebrate availability and consumption of ≥ 80 mm total length coastal cutthroat trout in stream study sections of Camp Creek, Tucua Creek, and North Fork Ecola Creek of the Oregon Coast Range. Numbers in parentheses indicate \pm standard error of the mean.

Variables	Camp Creek			Tucua Creek			North Fork Ecola Creek		
	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed
Benthos (dry mg•m ⁻²)									
Summer	2785 (734)	2035 (135)	2069 (339)	3144 (495)	4721 (1371)	4404 (1025)	1787 (488)	899 (379)	2122 (596)
Fall	3342 (1009)	3029 (863)	1565 (554)	2612 (731)	8473 (3237)	6563 (1389)	1266 (696)	362 (96)	1319 (767)
Winter	1736 (873)	793 (117)	781 (505)	1732 (777)	557 (83)	1417 (750)	623 (196)	479 (251)	384 (160)
Spring	1537 (412)	1510 (293)	1461 (331)	4349 (890)	6614 (2514)	2573 (1011)	809 (133)	1334 (898)	358 (88)
Drift (dry mg•m ⁻³ •h ⁻³)									
Summer	102.8 (76.4)	155.4 (81.0)	17.2 (0.2)	118.6 (16.7)	22.5 (0.1)	97.9 (21.5)	3.3 (2.0)	10.0 (2.0)	26.8 (2.8)
Fall	3.2 (2.1)	13.7 (0.7)	4.1 (1.8)	21.9 (9.3)	6.2 (4.3)	9.2 (4.0)	2.4 (1.8)	15.8 (4)	0.5 (0.03)
Winter	159.7 (28.0)	207.6 (67.4)	441.2 (142.5)	619.4 (514.2)	92.8 (26.8)	273.8 (217.5)	22.2 (1.0)	43.3 (13.3)	74.8 (58.3)
Spring	69.9 (7.8)	249.7 (87.0)	158.7 (48.2)	190.8 (93.9)	171.4 (43.9)	119.1 (58.1)	38.7 (27.0)	12.6 (2.0)	21.7 (2.2)
Allochthonous (dry mg•m ⁻² •d ⁻¹)									
Summer	137.6 (56.0)	38.7 (12.3)	30.5 (12.1)	52.1 (10.5)	56.7 (13.9)	63.6 (13.3)	70.1 (13.9)	53.4 (25.4)	79.2 (24.2)
Fall	45.6 (22.4)	8.4 (5.3)	31.0 (11.6)	58.2 (23.8)	37.3 (13.9)	44.4 (13.1)	10.7 (2.2)	5.6 (2.0)	9.3 (4.4)
Winter	4.4 (2.3)	3.1 (2.2)	7.4 (2.1)	3.3 (0.9)	11.2 (3.0)	13.7 (11.1)	11.4 (1.4)	2.7 (0.8)	8.4 (1.5)
Spring	9.6 (4.0)	2.8 (1.1)	13.9 (6.1)	5.8 (2.4)	1.7 (0.8)	4.3 (1.6)	10.5 (2.3)	15.9 (8.9)	11.2 (3.8)
Diet (dry mg•fish)									
Summer	20.2 (11.6)	8.7 (4.8)	5.3 (1.8)	9.3 (2.4)	3.7 (0.9)	4.6 (1.3)	4.9 (1.6)	1.7 (0.5)	9.7 (2.4)
Fall	5.9 (3.8)	4.7 (3.8)	2.9 (1.2)	10.2 (6.9)	5.7 (4.2)	1.4 (0.4)	5.6 (2.3)	3.3 (0.9)	2.0 (0.6)
Winter	16.7 (5.8)	10.3 (3.5)	6.3 (2.1)	5.3 (1.3)	14.0 (4.1)	3.2 (0.9)	9.8 (4.9)	1.5 (0.4)	5.1 (1.2)
Spring	17.3 (4.0)	37.6 (8.3)	25.0 (5.2)	24.2 (6.8)	23.2 (4.9)	39.2 (6.9)	10.2 (2.9)	7.5 (2.2)	11.9 (1.6)

Table A.2. Seasonal changes in terrestrial invertebrate availability and consumption of ≥ 80 mm total length coastal cutthroat trout in stream study sections of Camp Creek, Tucua Creek, and North Fork Ecola Creek of the Oregon Coast Range. Numbers in parentheses indicate \pm standard error of the mean.

Variables	Camp Creek			Tucua Creek			North Fork Ecola Creek		
	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed
Benthos									
(dry $\text{mg}\cdot\text{m}^{-2}$)									
Summer	---	---	---	---	---	---	---	---	---
Fall	---	---	---	---	---	---	---	---	---
Winter	---	---	---	---	---	---	---	---	---
Spring	---	---	---	---	---	---	---	---	---
Drift									
(dry $\text{mg}\cdot\text{m}^{-3}\cdot\text{h}^{-3}$)									
Summer	1.1 (1.1)	10.0 (1.4)	12.4 (4.4)	31.0 (15.9)	9.4 (3.9)	12.4 (0.1)	42.0 (38.1)	32.0 (23.9)	4.2 (0.01)
Fall	4.7 (2.3)	0.9 (0.5)	1.4 (0.01)	0.9 (0.9)	3.0 (0.3)	20.1 (18.7)	1.9 (1.7)	7.1 (7.1)	0.5 (0.5)
Winter	1.7 (1.3)	4.0 (0.01)	4.2 (4.0)	2.2 (2.2)	0.7 (0.7)	8.9 (8.7)	1.2 (0.2)	3.5 (2.9)	1.1 (0.3)
Spring	2.0 (1.0)	18.6 (14.7)	11.7 (9.5)	28.2 (9.2)	4.4 (1.3)	20.8 (.04)	10.6 (9.6)	30.6 (30.6)	2.0 (2.0)
Allochthonous									
(dry $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)									
Summer	69.1 (11.8)	65.8 (22.6)	46.5 (7.6)	60.4 (12.4)	61.5 (24.7)	60.7 (12.7)	31.2 (8.0)	16.9 (9.6)	31.9 (15.3)
Fall	8.2 (2.5)	76.3 (57.3)	103.7 (50.8)	46.9 (13.2)	19.1 (4.2)	18.6 (4.9)	9.9 (2.2)	12.8 (6.0)	5.4 (1.2)
Winter	3.8 (1.5)	2.2 (0.6)	2.4 (0.6)	14.5 (2.4)	8.4 (1.6)	14.6 (3.6)	7.7 (5.9)	5.0 (1.6)	0.3 (0.2)
Spring	5.3 (1.9)	10.9 (9.6)	19.2 (7.5)	2.3 (0.7)	1.2 (0.8)	4.5 (2.5)	23.3 (3.6)	9.8 (3.1)	20.0 (5.8)
Diet									
(dry $\text{mg}\cdot\text{fish}$)									
Summer	24.5 (7.8)	10.2 (3.9)	10.7 (5.1)	11.6 (4.8)	7.6 (3.2)	3.3 (1.6)	1.5 (0.6)	3.2 (2.6)	4.8 (1.8)
Fall	11.6 (8.1)	2.7 (1.6)	27.9 (13.8)	5.7 (2.0)	5.6 (3.7)	1.1 (0.6)	17.1 (6.7)	14.6 (6.4)	3.8 (1.8)
Winter	0.6 (0.5)	0.4 (0.3)	0.7 (0.7)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	1.5 (1.0)	0.9 (0.4)	0.1 (0.1)
Spring	7.1 (2.5)	16.9 (6.9)	4.1 (2.2)	9.1 (2.8)	4.3 (1.4)	4.5 (1.6)	12.0 (6.3)	7.4 (2.5)	4.3 (2.8)

Table A.3. Seasonal changes in total invertebrate availability and consumption of ≥ 80 mm total length coastal cutthroat trout in stream study sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek of the Oregon Coast Range. Numbers in parentheses indicate \pm standard error of the mean.

Variables	Camp Creek			Tucca Creek			North Fork Ecola Creek		
	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed
Benthos (dry $\text{mg}\cdot\text{m}^{-2}$)									
Summer	2785 (734)	2035 (135)	2069 (339)	3144 (495)	4721 (1371)	4404 (1025)	1787 (488)	899 (379)	2122 (596)
Fall	3342 (1009)	3029 (863)	1565 (554)	2612 (731)	8473 (3237)	6563 (1389)	1266 (696)	362 (96)	1319 (767)
Winter	1736 (873)	793 (117)	781 (505)	1732 (777)	557 (83)	1417 (750)	623 (196)	479 (251)	384 (160)
Spring	1537 (412)	1510 (293)	1461 (331)	4349 (890)	6614 (2514)	2573 (1011)	809 (133)	1334 (898)	358 (88)
Drift (dry $\text{mg}\cdot\text{m}^{-3}\cdot\text{h}^{-3}$)									
Summer	105.7 (78.6)	168.1 (85.1)	29.6 (4.6)	45.7 (35.7)	42.0 (25.9)	31.8 (2.0)	151.1 (2.3)	32.2 (3.5)	113.4 (19.4)
Fall	7.8 (0.3)	14.6 (1.2)	5.5 (1.8)	23.3 (8.9)	9.2 (4.0)	29.9 (15.3)	4.3 (1.2)	22.9 (6.7)	22.9 (6.7)
Winter	163.8 (28.8)	229.7 (67.5)	475.2 (162.6)	638.9 (529.6)	94.3 (25.4)	286.2 (227.6)	23.4 (0.8)	52.9 (22.2)	76.0 (58.5)
Spring	72.0 (9.0)	270.2 (102.4)	179.8 (46.3)	268.3 (151.8)	178.1 (45.7)	140.2 (57.8)	39.8 (27.4)	18.0 (7.2)	35.0 (7.5)
Allochthonous (dry $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)									
Summer	219.3 (54.5)	113.5 (31.0)	85.2 (17.8)	124.4 (16.5)	127.7 (30.5)	137.2 (20.6)	111.3 (14.9)	77.8 (27.3)	116.9 (33.6)
Fall	55.1 (22.2)	86.1 (55.5)	137.4 (52.0)	108.1 (23.3)	58.6 (13.3)	66.5 (12.4)	22.4 (2.5)	18.5 (6.9)	23.9 (8.2)
Winter	9.2 (2.1)	5.8 (2.5)	10.8 (2.0)	12.5 (6.3)	19.0 (3.4)	14.8 (11.0)	27.3 (3.5)	11.2 (2.2)	23.6 (4.3)
Spring	15.0 (4.4)	13.7 (10.3)	38.2 (11.7)	8.5 (2.6)	2.9 (1.1)	10.8 (2.7)	34.6 (4.7)	25.8 (11.4)	32.1 (9.1)
Diet (dry $\text{mg}\cdot\text{fish}$)									
Summer	46.1 (14.3)	23.8 (9.0)	18.4 (5.6)	22.1 (7.1)	12.5 (3.2)	8.3 (2.5)	7.1 (2.2)	5.3 (2.5)	15.4 (3.8)
Fall	17.8 (9.8)	7.4 (4.0)	30.9 (13.6)	16.1 (6.9)	11.3 (5.3)	2.6 (0.7)	23.2 (7.3)	18.1 (6.8)	5.9 (2.3)
Winter	18.9 (5.8)	20.4 (12.6)	8.4 (2.9)	5.4 (1.5)	14.2 (4.1)	3.5 (0.9)	13.1 (5.5)	2.6 (0.7)	6.8 (2.0)
Spring	24.8 (5.1)	70.0 (16.8)	29.1 (5.8)	34.6 (7.0)	27.9 (5.5)	43.8 (7.2)	22.4 (7.7)	19.7 (5.5)	16.6 (3.4)

Table. A.4. Invertebrate taxa collected in the benthos with Surber nets in stream study sections of the Oregon Coast Range from July 2001 through April 2002, and their relative biomass (dry mass•mg•m⁻²) and abundance (organisms•m⁻²). Numbers in parentheses indicate relative percent

Taxon	Biomass	Abundance
Annelida		
Oligochaeta	36.5 (1.6)	182.8 (5.3)
Arthropoda		
Acharina		
Acari	2.3 (0.1)	10.2 (0.3)
Decapoda	53.8 (2.4)	0.7 (<0.1)
Insecta		
Coleoptera		
Chrysomelidae	0.1 (<0.1)	0.1 (<0.1)
Dryopidae	<0.1 (<0.1)	0.1 (<0.1)
Dytiscidae	2.1 (0.1)	2.2 (0.1)
Elmidae	78.8 (3.5)	224.2 (6.5)
Hydrophilidae	0.5 (<0.1)	1.1 (<0.1)
Psphenidae	0.3 (<0.1)	0.7 (<0.1)
Scirtidae	0.6 (<0.1)	0.1 (<0.1)
Staphylinidae	0.4 (<0.1)	0.6 (<0.1)
Unknown	<0.1 (<0.1)	0.1 (<0.1)
Collembola	0.1 (<0.1)	1.8 (0.1)
Diptera		
Blepharceridae	0.1 (<0.1)	0.2 (<0.1)
Ceratopogonidae	4.6 (0.2)	26.5 (0.8)
Chironomidae	16.7 (0.7)	472.5 (13.6)
Culicidae	<0.1 (<0.1)	0.1 (<0.1)
Dixidae	0.7 (<0.1)	5.0 (0.1)
Dolichopididae	0.8 (<0.1)	0.5 (<0.1)
Empididae	4.2 (0.2)	15.3 (0.4)
Ephydriidae	14.0 (0.6)	4.5 (0.1)
Pelechorynchidae	27.2 (1.2)	16.8 (0.5)
Phoridae	<0.1 (<0.1)	0.2 (<0.1)
Ptychopteridae	2.4 (0.1)	10.2 (0.3)
Simuliidae	6.9 (0.3)	38.6 (1.1)
Stratiomyiidae	0.1 (<0.1)	0.3 (<0.1)
Tabanidae	17.1 (0.7)	1.2 (<0.1)
Tipulidae	688.8 (30.2)	42.1 (1.2)
Unknown	0.6 (<0.1)	1.0 (<0.1)
Ephemeroptera		
Amelitidae	10.7 (0.5)	14.8 (0.4)
Baetidae	60.5 (2.7)	349.4 (10.1)

Taxon	Biomass	Abundance
Ephemerillidae	31.9 (1.4)	150.6 (4.3)
Ephemeridae	2.3 (0.1)	44.8 (1.3)
Heptageniidae	191.4 (8.4)	484.1 (13.9)
Leptophlebiidae	10.8 (0.5)	221.5 (6.4)
Hemiptera		
Gerridae	1.8 (0.1)	0.3 (<0.1)
Macroveliidae	<0.1 (<0.1)	0.2 (<0.1)
Ochteridae	<0.1 (<0.1)	<0.1 (<0.1)
Salidae	0.1 (<0.1)	0.8 (0.1)
Veliidae	<0.1 (<0.1)	1.5 (<0.1)
Unknown	<0.1 (<0.1)	0.2 (<0.1)
Neuroptera		
Corydalidae	0.1 (<0.1)	0.1 (<0.1)
Sialidae	0.1 (<0.1)	0.4 (<0.1)
Odonata		
Gomphidae	11.3 (0.5)	17.3 (0.5)
Plecoptera		
Capniidae	2.6 (0.1)	13.3 (0.4)
Chloroperlidae	52.4 (2.3)	190.2 (5.5)
Leuctridae	5.8 (0.3)	28.5 (0.8)
Nemouridae	11.5 (0.5)	151.4 (4.4)
Peltoperlidae	29.6 (1.3)	38.3 (1.1)
Perlidae	429.2 (18.8)	149.3 (4.3)
Perlodidae	51.2 (2.2)	54.4 (1.6)
Pteronarcyidae	178.8 (7.9)	1.9 (0.1)
Taeniopterygidae	0.5 (<0.1)	6.6 (0.2)
Unknown	<0.1 (<0.1)	0.1 (<0.1)
Trichoptera		
Brachycentridae	4.9 (0.2)	69.8 (2.0)
Glossosomatidae	34.4 (1.5)	102.4 (2.9)
Hydropsychiidae	11.7 (0.5)	27.6 (0.8)
Hydroptilidae	5.6 (0.2)	29.0 (0.8)
Lepidostomatidae	4.4 (0.2)	47.6 (1.4)
Limnephilidae	38.3 (1.7)	49.0 (1.4)
Odontoceridae	0.9 (<0.1)	0.6 (<0.1)
Philopotamidae	4.6 (0.2)	13.4 (0.4)
Polycentropodidae	0.4 (<0.1)	1.9 (0.1)
Psychomyiidae	<0.1 (<0.1)	0.1 (<0.1)
Rhyacophilidae	79.8 (3.5)	82.0 (2.4)
Uenoidae	0.2 (<0.1)	0.1 (<0.1)
Unkown	<0.1 (<0.1)	0.6 (<0.1)

Taxon	Biomass	Abundance
Mollusca		
Gastropoda		
Pleuroceridae	24.1 (1.1)	2.1 (0.1)
Pelecypoda	0.8 (<0.1)	6.7 (0.3)
Nemertea	24.9 (1.1)	10.0 (0.3)
Platyhelminthes		
Turbellaria	0.4 (<0.1)	2.1 (0.1)

Table A.5. Allochthonous invertebrate input collected in pan traps in stream study sections of the Oregon Coast Range from July 2001 through April 2002, and their relative biomass (dry mass•mg•m⁻²) and abundance (organisms•m⁻²). Numbers in parentheses indicate relative percent.

Taxon	Biomass	Abundance
Arthropoda		
Acharina		
Acari	<0.1 (<0.1)	0.2 (0.3)
Araneae		
Agelenida	<0.1 (<0.1)	<0.1 (<0.1)
Anyphaenida	0.1 (0.1)	0.1 (<0.1)
Clubionidae	0.1 (0.2)	0.1 (0.1)
Dictynidae	<0.1 (<0.1)	<0.1 (<0.1)
Linyphiidae	0.1 (0.2)	0.4 (0.6)
Philodromidae	<0.1 (<0.1)	<0.1 (<0.1)
Salticidae	0.1 (0.1)	<0.1 (0.1)
Tetragnathidae	0.6 (1.1)	0.3 (0.4)
Theridiidae	<0.1 (0.1)	0.3 (0.5)
Thomisidae	<0.1 (<0.1)	<0.1 (<0.1)
Uloboridae	<0.1 (<0.1)	<0.1 (<0.1)
Unknown	0.2 (0.3)	0.6 (0.9)
Opiliones		
Palpatores	0.1 (0.1)	0.1 (0.1)
Diplopoda		
Polydesimida	0.1 (0.3)	<0.1 (<0.1)
Isopoda	<0.1 (<0.1)	<0.1 (<0.1)
Insecta		
Unknown	2.0 (3.5)	0.1 (0.1)
Coleoptera		
Anobiidae	<0.1 (0.1)	<0.1 (<0.1)
Cantharidae	0.7 (1.3)	0.3 (0.4)
Carabidae	<0.1 (0.1)	<0.1 (<0.1)
Cerambycidae	0.5 (1.0)	<0.1 (<0.1)
Chrysomelidae	0.5 (0.8)	0.1 (0.1)
Coccinellidae	<0.1 (<0.1)	<0.1 (<0.1)
Derodontidae	<0.1 (<0.1)	<0.1 (<0.1)
Dystiscidae	<0.1 (<0.1)	<0.1 (<0.1)
Elateridae	1.3 (2.4)	0.1 (0.1)
Elmidae	0.2 (0.3)	0.5 (0.7)
Hydrophilidae	<0.1 (<0.1)	<0.1 (<0.1)
Lathridiidae	<0.1 (<0.1)	0.1 (0.1)
Psphenidae	0.2 (0.3)	0.2 (0.2)

Taxon	Biomass	Abundance
Ptilidae	<0.1 (<0.1)	<0.1 (<0.1)
Scolytidae	<0.1 (<0.1)	<0.1 (<0.1)
Staphylinidae	0.8 (1.4)	1.2 (1.7)
Tenebrionidae	<0.1 (0.1)	<0.1 (<0.1)
Unknown	0.7 (1.3)	0.3 (0.5)
Collembola		
Entomobryiidae	0.2 (0.3)	0.5 (0.7)
Poduridae	<0.1 (<0.1)	<0.1 (0.1)
Sminthuridae	<0.1 (<0.1)	0.1 (0.2)
Unknown	<0.1 (<0.1)	0.1 (0.1)
Diptera		
Asilidae	1.5 (2.7)	0.1 (0.1)
Calliphoridae	<0.1 (0.1)	<0.1 (<0.1)
Cecidomyiidae	0.2 (0.3)	1.6 (2.3)
Ceratopogonidae	<0.1 (0.1)	0.5 (0.7)
Chironomidae	1.2 (2.2)	9.1 (13.5)
Cutereberidae	<0.1 (0.1)	<0.1 (<0.1)
Dixidae	0.7 (1.2)	1.8 (2.6)
Dolichopodidae	0.7 (1.1)	0.5 (0.7)
Drosophilidae	<0.1 (<0.1)	0.1 (<0.1)
Empididae	1.9 (3.3)	9.6 (14.1)
Lonchopteridae	<0.1 (<0.1)	<0.1 (<0.1)
Muscidae	0.9 (1.5)	0.6 (0.9)
Mycetophilidae	2.8 (5.0)	17.8 (26.3)
Oestridae	<0.1 (0.1)	<0.1 (<0.1)
Phoridae	0.3 (0.6)	1.8 (2.7)
Psychodidae	0.1 (0.2)	0.6 (0.9)
Rhagionidae	0.1 (0.2)	<0.1 (<0.1)
Sarcophagidae	<0.1 (<0.1)	<0.1 (<0.1)
Scatopsidae	<0.1 (<0.1)	0.1 (0.1)
Sciaridae	1.0 (1.7)	3.9 (5.7)
Sciomyzidae	0.6 (1.0)	0.8 (1.2)
Simuliidae	0.1 (0.1)	0.1 (0.2)
Syrphidae	0.1 (0.2)	0.1 (0.1)
Tanyderidae	0.1 (0.2)	0.1 (0.2)
Thereviidae	0.3 (0.6)	0.1 (0.2)
Tipulidae	4.3 (7.7)	3.0 (4.5)
Unknown	1.4 (2.5)	1.8 (2.6)
Ephemeroptera		
Amelitidae	0.4 (0.6)	0.1 (0.1)
Baetidae	0.2 (0.3)	0.1 (0.1)

Taxon	Biomass	Abundance
Ephemerillidae	<0.1 (<0.1)	<0.1 (0.1)
Heptageniidae	0.6 (1.0)	0.1 (0.2)
Leptophlebiidae	0.3 (1.0)	0.1 (0.2)
Unknown	1.3 (2.9)	0.6 (0.9)
Hemiptera		
Gerridae	0.7 (1.3)	<0.1 (<0.1)
Miridae	<0.1 (<0.1)	<0.1 (0.1)
Pentatomidae	0.1 (0.2)	0.1 (0.1)
Saldidae	<0.1 (<0.1)	<0.1 (<0.1)
Tingidae	<0.1 (<0.1)	<0.1 (<0.1)
Unknown	<0.1 (<0.1)	<0.1 (<0.1)
Homoptera		
Aphididae	0.3 (0.5)	0.7 (1.0)
Cercopidae	<0.1 (<0.1)	<0.1 (<0.1)
Cicadellidae	0.2 (0.4)	0.4 (0.5)
Delphacidae	<0.1 (<0.1)	<0.1 (<0.1)
Membracidae	0.3 (0.5)	0.1 (0.1)
Psyllidae	<0.1 (<0.1)	<0.1 (<0.1)
Unknown	<0.1 (<0.1)	<0.1 (<0.1)
Hymenoptera		
Braconidae	0.1 (0.2)	0.2 (0.3)
Ceraphronidae	<0.1 (<0.1)	0.1 (0.1)
Cynipidae	<0.1 (<0.1)	<0.1 (<0.1)
Diapriidae	<0.1 (<0.1)	0.1 (0.2)
Encyrtidae	<0.1 (<0.1)	<0.1 (<0.1)
Eulophidae	<0.1 (<0.1)	<0.1 (<0.1)
Eurytomidae	<0.1 (<0.1)	<0.1 (<0.1)
Formicidae	0.5 (0.9)	0.1 (0.2)
Ichneumonidae	0.3 (0.5)	0.1 (0.3)
Mymaridae	<0.1 (<0.1)	0.1 (0.1)
Platygasteridae	<0.1 (<0.1)	<0.1 (<0.1)
Proctotrupidae	<0.1 (<0.1)	0.1 (0.1)
Pteromolidae	<0.1 (<0.1)	0.1 (0.1)
Scelionidae	<0.1 (<0.1)	<0.1 (<0.1)
Tenthredinidae	0.6 (1.1)	0.1 (0.1)
Vespidae	1.0 (1.7)	<0.1 (<0.1)
Unknown	0.2 (0.4)	<0.1 (<0.1)
Lepidoptera		
Geometridae	1.5 (2.7)	0.1 (0.1)
Unknown	1.6 (2.8)	0.1 (0.3)

Taxon	Biomass	Abundance
Neuroptera		
Hemerobiidae	0.2 (0.3)	0.1 (0.1)
Odonata		
Gomphidae	1.7 (3.1)	<0.1 (<0.1)
Orthoptera		
Gryllacrididae	0.9 (1.7)	0.1 (0.1)
Plecoptera		
Chloroperlidae	1.1 (1.9)	0.7 (1.0)
Leuctridae	0.3 (0.6)	0.3 (0.4)
Nemouridae	0.9 (1.5)	0.5 (0.7)
Perlodidae	2.7 (4.7)	0.1 (0.2)
Taeniopterygidae	0.1 (0.1)	<0.1 (<0.1)
Unknown	0.3 (0.6)	<0.1 (<0.1)
Psocoptera	0.1 (0.2)	0.6 (0.9)
Thysanura		
Thripidae	<0.1 (<0.1)	<0.1 (0.1)
Trichoptera		
Brachycentridae	0.1 (0.1)	<0.1 (0.1)
Calamoceratidae	0.2 (0.3)	<0.1 (<0.1)
Glossosomatidae	0.2 (0.4)	<0.1 (<0.1)
Heliopsychidae	0.2 (0.4)	0.1 (0.1)
Hydropsychidae	1.0 (1.9)	0.1 (0.2)
Lepidostomatidae	0.1 (0.1)	<0.1 (<0.1)
Limnephilidae	3.2 (5.7)	0.1 (0.2)
Philopotamidae	0.2 (0.4)	0.1 (0.2)
Phyrgaenidae	0.1 (0.2)	0.1 (0.1)
Polycentropodidae	0.4 (0.8)	0.1 (0.2)
Psychomyiidae	0.2 (0.3)	0.2 (0.2)
Rhyacophilidae	3.6 (6.4)	0.6 (0.9)
Unknown	0.6 (1.1)	0.2 (0.3)
Nemertea	0.1 (0.2)	<0.1 (<0.1)

Table A.6. Invertebrate taxa ingested by coastal cutthroat trout in stream study sections of the Oregon Coast Range from July 2001 through April 2002, and their relative biomass (dry mass•mg•m⁻²) and abundance (organisms•m⁻²). Numbers in parentheses indicate relative percent.

Taxon	Biomass	Abundance
Annelida		
Oligochaeta	0.8 (4.2)	0.2 (1.1)
Arthropoda		
Acharina		
Acari	0.2 (0.1)	0.4 (0.3)
Araneae	1.0 (4.7)	0.3 (1.9)
Chelonithida	<0.1 (<0.1)	<0.1 (0.1)
Opiliones		
Palpatores	<0.1 (0.1)	<0.1 (0.1)
Chilopoda		
Geophilomorpha	0.2 (1.1)	<0.1 (0.1)
Decapoda		
Atascidae	0.5 (2.6)	<0.1 (0.1)
Diplopoda		
Chordeumida	0.2 (0.1)	<0.1 (0.2)
Polydesimida	0.5 (2.7)	<0.1 (0.3)
Isopoda	0.1 (0.4)	<0.1 (0.2)
Insecta		
Coleoptera		
Amphizoidae	<0.1 (<0.1)	<0.1 (<0.1)
Anobiidae	<0.1 (<0.1)	<0.1 (0.1)
Cantharidae	0.1 (<0.1)	<0.1 (0.2)
Carabidae	0.4 (2.3)	<0.1 (0.3)
Cerambycidae	0.1 (0.5)	<0.1 (0.1)
Chrysomelidae	0.1 (0.7)	<0.1 (0.4)
Dystiscidae	0.2 (0.1)	0.1 (0.7)
Elateridae	0.2 (0.8)	<0.1 (0.1)
Elmidae	0.1 (0.4)	<0.1 (0.2)
Hydrophilidae	0.1 (0.5)	<0.1 (0.2)
Mordellidae	<0.1 (<0.1)	<0.1 (0.1)
Staphylinidae	0.5 (2.6)	0.2 (1.4)
Unknown	0.5 (2.6)	0.2 (1.2)
Collembola	<0.1 (0.1)	0.2 (1.4)
Diptera		
Asilidae	0.4 (2.2)	<0.1 (0.3)
Blephariceridae	<0.1 (<0.1)	<0.1 (0.1)
Ceratopogonidae	<0.1 (0.2)	0.2 (1.3)
Chironomidae	0.5 (2.5)	3.9 (26.4)

Taxon	Biomass	Abundance
Dixidae	<0.1 (0.2)	0.1 (0.8)
Dolichopodidae	<0.1 (<0.1)	<0.1 (0.1)
Empididae	0.1 (0.5)	0.2 (1.4)
Ephydriidae	<0.1 (<0.1)	<0.1 (<0.1)
Mycetophilidae	<0.1 (0.2)	<0.1 (0.6)
Pelecorhynchidae	<0.1 (0.3)	<0.1 (0.2)
Phoridae	<0.1 (<0.1)	<0.1 (0.2)
Sciaridae	<0.1 (0.1)	0.2 (1.0)
Sciomyzidae	<0.1 (<0.1)	<0.1 (0.1)
Simuliidae	<0.1 (0.1)	0.3 (2.2)
Stratiomyiidae	0.1 (0.5)	<0.1 (0.6)
Tipulidae	0.6 (2.8)	0.2 (1.1)
Unknown	0.1 (0.7)	0.2 (0.3)
Ephemeroptera		
Amelitidae	0.3 (1.7)	0.4 (2.7)
Baetidae	0.9 (4.6)	1.7 (11.5)
Ephemerillidae	0.3 (1.7)	0.2 (1.6)
Heptageniidae	1.9 (9.9)	1.0 (7.1)
Leptophlebiidae	0.1 (0.3)	0.2 (1.6)
Unknown	0.1 (0.3)	0.1 (0.9)
Hemiptera		
Gerridae	0.2 (0.9)	<0.1 (0.1)
Miridae	<0.1 (<0.1)	<0.1 (<0.1)
Pentatomidae	0.1 (0.3)	<0.1 (0.1)
Saldidae	<0.1 (<0.1)	<0.1 (0.1)
Unknown	<0.1 (0.1)	<0.1 (0.1)
Homoptera		
Aphididae	<0.1 (0.1)	<0.1 (0.3)
Cercopidae	<0.1 (0.1)	<0.1 (<0.1)
Cicadellidae	0.1 (0.7)	<0.1 (0.6)
Membracidae	0.5 (2.7)	0.1 (0.8)
Psyllidae	<0.1 (0.1)	<0.1 (<0.1)
Unknown	0.1 (0.5)	<0.1 (0.2)
Hymenoptera		
Braconidae	<0.1 (0.1)	<0.1 (0.1)
Diapriidae	<0.1 (<0.1)	<0.1 (0.1)
Formicidae	0.2 (0.9)	0.2 (1.5)
Ichneumonidae	<0.1 (0.2)	<0.1 (0.3)
Pteromolidae	<0.1 (<0.1)	<0.1 (0.1)
Unknown	<0.1 (0.3)	<0.1 (0.2)
Isoptera	<0.1 (0.2)	<0.1 (0.2)

Taxon	Biomass	Abundance
Lepidoptera	0.3 (1.4)	<0.1 (0.4)
Neuroptera		
Chrysopidae	<0.1 (0.1)	<0.1 (0.1)
Hemerobiidae	<0.1 (<0.1)	<0.1 (<0.1)
Sialidae	<0.1 (0.1)	<0.1 (<0.1)
Orthoptera		
Gryllacrididae	1.2 (6.2)	<0.1 (0.1)
Plecoptera		
Capniidae	0.1 (0.5)	0.1 (0.8)
Chloroperlidae	<0.1 (0.4)	0.1 (0.7)
Leuctridae	0.1 (0.5)	0.1 (0.7)
Nemouridae	0.3 (1.4)	0.4 (3.0)
Peltoperlidae	<0.1 (0.2)	<0.1 (0.2)
Perlidae	1.6 (8.4)	0.1 (0.9)
Perlodidae	<0.1 (0.3)	<0.1 (0.1)
Pteronarcyidae	<0.1 (<0.1)	<0.1 (<0.1)
Unknown	0.1 (0.6)	0.1 (1.0)
Pscoptera	<0.1 (<0.1)	<0.1 (0.5)
Thysanura	<0.1 (0.2)	<0.1 (0.1)
Trichoptera		
Brachycentridae	0.4 (2.2)	0.3 (2.1)
Glossosomatidae	0.1 (0.4)	<0.1 (0.4)
Hydropsychidae	0.3 (1.3)	<0.1 (0.4)
Hydroptilidae	<0.1 (<0.1)	<0.1 (0.1)
Lepidostomatidae	0.1 (0.6)	0.2 (1.4)
Limnephilidae	0.9 (4.4)	0.8 (5.4)
Philopotamidae	0.1 (0.4)	0.1 (0.9)
Phyrgieinidae	<0.1 (<0.1)	<0.1 (<0.1)
Polycentropodidae	0.1 (0.3)	<0.1 (0.3)
Psychomyiidae	<0.1 (<0.1)	<0.1 (<0.1)
Rhyacophilidae	0.5 (2.4)	0.2 (1.1)
Unknown	0.4 (1.9)	0.2 (1.4)
Mollusca		
Gastropoda	0.2 (0.9)	<0.1 (<0.1)
Platyhelminthes		
Turbellaria	<0.1 (<0.1)	<0.1 (<0.1)

Table A.7. Seasonal changes in taxonomic composition (mg dry mass·m⁻²) of invertebrates collected from benthic Surber samples in deciduous, conifer, and mixed stream study sections of the Oregon Coast Range from July 2001 through April 2002. Numbers in parentheses indicate abundance (organisms·m⁻²).

Vegetation	Taxa	Summer	Fall	Winter	Spring
Deciduous	Acari	0.0 (0.0)	2.0 (55.0)	0.5 (12.0)	5.5 (105.9)
	Coleoptera	80.7 (380.3)	137.2 (389.3)	59.3 (61.6)	85.5 (248.2)
	Collembola	0.2 (4.2)	0.1 (4.2)	0.0 (0.6)	0.3 (1.8)
	Decapoda	186.6 (0.6)	259.8 (2.4)	0.0 (0.0)	1.1 (0.6)
	Diptera	441.8 (1254.6)	1140.7 (578.3)	670.7 (303.2)	749.6 (723.0)
	Ephemeroptera	246.3 (1232.5)	161.4 (1128.4)	188.8 (1100.3)	568.7 (1651.7)
	Gastropoda	0.4 (2.4)	43.8 (1.8)	0.3 (3.0)	0.0 (0.0)
	Hemiptera	0.9 (4.2)	1.6 (9.6)	0.1 (0.1)	0.1 (0.6)
	Nemertea	0.0 (0.0)	69.5 (32.9)	4.6 (9.6)	7.1 (8.4)
	Neuroptera	0.0 (0.0)	0.6 (3.0)	0.2 (0.6)	0.0 (0.0)
	Odonata	1.8 (19.7)	2.6 (20.3)	1.7 (11.4)	1.7 (8.4)
	Oligochaeta	1.4 (16.2)	31.3 (20.6)	71.9 (379.7)	59.1 (238.6)
	Pelecypoda	0.1 (3.0)	0.2 (4.2)	2.2 (17.9)	0.4 (9.6)
	Plecoptera	1216.6 (1148.8)	370.5 (642.3)	447.6 (405.4)	619.0 (444.9)
	Trichoptera	293.8 (619.5)	185.8 (776.8)	114.3 (222.5)	132.7 (178.8)
	Turbellaria	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (6.0)
	Unknown	0.9 (1.8)	2.2 (3.0)	0.0 (0.0)	0.0 (0.0)
Conifer	Acari	0.0 (0.0)	2.8 (98.1)	0.6 (10.2)	0.0 (0.0)
	Coleoptera	62.3 (251.8)	129.2 (400.1)	16.4 (40.1)	144.5 (226.6)
	Collembola	0.2 (3.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Decapoda	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Diptera	1290.9 (1335.3)	532.3 (790.0)	195.6 (178.8)	758.5 (471.8)
	Ephemeroptera	284.0 (1106.9)	247.7 (1866.3)	126.4 (581.9)	483.6 (1096.1)
	Gastropoda	0.6 (1.2)	66.2 (5.4)	0.0 (1.2)	0.4 (1.2)
	Hemiptera	0.1 (4.8)	0.8 (4.8)	0.0 (0.0)	0.2 (0.6)
	Nemertea	0.0 (0.0)	5.0 (13.8)	11.5 (12.0)	10.8 (7.8)
	Neuroptera	0.0 (0.0)	0.3 (0.6)	0.2 (0.6)	0.8 (0.6)
	Odonata	1.8 (24.5)	2.6 (20.3)	1.7 (11.4)	1.7 (8.4)
	Oligochaeta	1.4 (16.2)	9.4 (48.4)	1.2 (15.6)	2.2 (21.5)
	Pelecypoda	0.1 (1.2)	1.7 (7.8)	0.5 (4.2)	0.2 (4.2)
	Plecoptera	674.3 (835.4)	2584.0 (1184.6)	179.0 (185.4)	1597.9 (470.0)
	Trichoptera	280.6 (435.9)	318.3 (935.5)	50.9 (101.1)	95.8 (139.3)
	Turbellaria	0.3 (1.8)	0.0 (0.0)	0.0 (0.0)	1.2 (8.4)
	Unknown	2.2 (3.0)	0.4 (1.2)	0.0 (0.0)	0.0 (0.0)

Vegetation	Taxa	Summer	Fall	Winter	Spring
Mixed	Acari	3.7 (126.2)	2.3 (64.0)	0.1 (1.8)	1.8 (36.5)
	Coleoptera	101.9 (356.4)	136.7 (435.9)	8.3 (23.9)	39.2 (136.9)
	Collembola	0.0 (1.2)	0.0 (1.2)	0.0 (0.6)	0.1 (2.4)
	Decapoda	51.3 (1.8)	52.9 (1.8)	92.9 (0.6)	0.0 (0.0)
	Diptera	1132.2 (897.6)	1614.5 (528.6)	290.2 (143.5)	586.2 (401.3)
	Ephemeroptera	421.0 (1700.7)	310.8 (1622.4)	164.9 (912.5)	497.0 (1217.5)
	Gastropoda	171.6 (7.77)	0.0 (0.0)	5.7 (1.2)	0.0 (0.0)
	Hemiptera	21.2 (7.8)	0.3 (1.2)	0.0 (0.0)	0.0 (0.0)
	Nemertea	0.0 (0.0)	129.5 (26.3)	53.2 (5.4)	7.5 (4.2)
	Neuroptera	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.6)
	Odonata	1.5 (14.4)	97.6 (15.6)	13.4 (4.2)	0.5 (4.2)
	Oligochaeta	14.0 (4.8)	39.4 (256.5)	34.4 (563.3)	30.7 (83.1)
	Pelecypoda	0.4 (5.4)	1.3 (3.6)	1.8 (16.2)	0.2 (3.0)
	Plecoptera	500.7 (847.4)	581.4 (863.5)	149.2 (239.8)	217.5 (340.9)
	Trichoptera	442.8 (582.5)	182.2 (842.0)	43.2 (150.7)	81.8 (99.9)
	Turbellaria	0.9 (3.6)	0.0 (0.0)	0.0 (0.0)	0.3 (1.8)
	Unknown	1.9 (3.0)	0.8 (0.6)	0.0 (0.0)	0.2 (0.6)

Table A8. Seasonal changes in taxonomic composition ($\text{mg dry mass} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) of invertebrates collected from allochthonous pan traps in deciduous, conifer, and mixed stream study sections of the Oregon Coast Range from July 2001 through April 2002. Numbers in parentheses indicate abundance ($\text{organisms} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$).

Vegetation	Taxa	Summer	Fall	Winter	Spring
Deciduous	Aquatic				
	Coleoptera	0.8 (0.8)	0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Collembola	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Diptera	13.3 (26.2)	6.6 (9.4)	6.6 (12.5)	3.4 (9.1)
	Ephemeroptera	9.6 (3.9)	2.1 (0.4)	0.0 (0.0)	3.2 (0.5)
	Hemiptera	0.0 (0.0)	6.3 (0.2)	0.0 (0.0)	0.0 (0.0)
	Odonata	20.5 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Plecoptera	13.0 (5.2)	4.1 (0.6)	0.1 (0.1)	0.8 (0.3)
	Trichoptera	31.5 (6.2)	23.2 (1.6)	0.0 (0.0)	0.9 (0.2)
	Terrestrial				
	Acari	<0.1 (0.4)	0.0 (0.0)	0.0 (0.0)	<0.1 (0.2)
	Araneida	2.9 (2.7)	1.7 (2.9)	0.2 (0.2)	0.5 (0.9)
	Coleoptera	15.0 (2.7)	0.7 (0.3)	<0.1 (<0.1)	4.7 (1.0)
	Collembola	0.1 (0.3)	0.3 (0.8)	0.1 (0.2)	0.1 (0.2)
	Diptera	20.7 (22.6)	8.2 (14.5)	7.1 (39.3)	4.1 (4.8)
	Hemiptera	0.2 (0.5)	0.3 (0.2)	0.0 (0.0)	0.0 (0.0)
	Homoptera	4.1 (3.2)	0.6 (0.8)	0.0 (0.0)	0.1 (0.2)
	Hymenoptera	1.3 (4.1)	1.3 (1.4)	<0.1 (<0.1)	0.1 (0.3)
	Isopoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Lepidoptera	4.7 (3.2)	3.5 (0.3)	1.6 (<0.1)	0.0 (0.0)
	Neuroptera	1.0 (0.2)	0.3 (1.1)	0.0 (0.0)	0.0 (0.0)
	Opiliones	0.2 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Orthoptera	1.8 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Polydesmida	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Psocoptera	0.2 (0.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Thysanura	<0.0 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Unknown				
	Coleoptera	1.5 (2.0)	0.7 (0.8)	0.7 (0.2)	0.3 (0.5)
	Diptera	9.8 (46.5)	2.0 (2.4)	0.6 (0.7)	0.2 (0.1)
	Miscellaneous	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)
Conifer	Aquatic				
	Coleoptera	1.1 (1.9)	0.0 (0.0)	0.7 (<0.1)	0.0 (0.0)
	Collembola	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Diptera	13.7 (14.3)	5.7 (6.1)	7.3 (2.8)	1.4 (6.2)
	Ephemeroptera	5.3 (2.1)	1.1 (0.4)	0.0 (0.0)	2.3 (0.2)

Vegetation	Taxa	Summer	Fall	Winter	Spring
	Hemiptera	0.1 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Odonata	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Plecoptera	8.7 (1.8)	4.0 (0.9)	1.4 (0.5)	3.4 (0.3)
	Trichoptera	21.4 (4.2)	7.6 (0.4)	0.0 (0.0)	0.0 (0.0)
	Terrestrial				
	Acari	<0.1 (0.2)	<0.1 (0.1)	0.2 (0.1)	0.0 (0.0)
	Araneida	2.4 (3.3)	0.4 (2.1)	0.4 (0.2)	0.9 (0.5)
	Coleoptera	9.6 (1.1)	0.2 (0.1)	0.1 (<0.1)	1.4 (0.1)
	Collembola	0.1 (0.4)	0.2 (0.8)	0.8 (0.3)	<0.1 (0.2)
	Diptera	18.7 (19.4)	6.0 (5.5)	17.8 (6.7)	2.2 (1.1)
	Hemiptera	0.1 (0.2)	0.3 (0.1)	0.0 (0.0)	0.0 (0.0)
	Homoptera	0.8 (1.2)	0.7 (1.2)	0.1 (<0.1)	0.1 (0.1)
	Hymenoptera	5.9 (2.0)	8.8 (0.5)	0.0 (0.0)	2.8 (0.1)
	Isopoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Lepidoptera	9.0 (0.7)	4.3 (0.3)	0.0 (0.0)	0.0 (0.0)
	Neuroptera	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Opiliones	0.2 (0.2)	<0.1 (0.1)	0.0 (0.0)	0.0 (0.0)
	Orthoptera	0.1 (0.1)	7.5 (0.2)	0.0 (0.0)	0.0 (0.0)
	Polydesmida	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Psocoptera	0.2 (1.2)	0.5 (1.7)	0.0 (0.0)	0.0 (0.0)
	Thysanura	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Unknown				
	Coleoptera	2.0 (3.6)	0.2 (0.4)	0.4 (0.2)	0.0 (0.0)
	Diptera	6.7 (19.5)	1.0 (1.0)	1.2 (0.4)	0.2 (0.1)
	Miscellaneous	0.0 (0.0)	0.5 (0.2)	0.1 (<0.1)	0.0 (0.0)
Mixed	Aquatic				
	Coleoptera	1.7 (5.1)	0.2 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Collembola	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Diptera	10.5 (38.6)	7.8 (5.3)	6.8 (20.7)	4.8 (16.5)
	Ephemeroptera	9.5 (3.6)	1.1 (0.1)	0.0 (0.0)	1.8 (0.4)
	Hemiptera	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	2.3 (0.1)
	Odonata	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Plecoptera	19.9 (5.2)	4.7 (0.3)	0.8 (0.9)	2.1 (0.9)
	Trichoptera	15.6 (5.2)	15.6 (0.9)	3.1 (0.3)	0.9 (0.3)
	Terrestrial				
	Acari	<0.1 (0.9)	<0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Araneida	3.8 (4.3)	0.7 (0.8)	<0.1 (0.3)	1.1 (1.5)
	Coleoptera	8.2 (3.0)	1.4 (0.4)	0.0 (0.0)	5.7 (3.1)
	Collembola	<0.1 (0.6)	0.5 (0.5)	0.1 (0.7)	0.4 (1.1)

Vegetation	Taxa	Summer	Fall	Winter	Spring
	Diptera	15.0 (23.0)	5.6 (3.7)	6.4 (72.8)	4.2 (19.5)
	Hemiptera	0.1 (0.5)	0.9 (0.1)	0.0 (0.0)	0.0 (0.0)
	Homoptera	2.4 (5.1)	1.0 (0.7)	<0.0 (0.1)	0.1 (0.2)
	Hymenoptera	11.9 (4.2)	0.2 (0.3)	0.0 (0.0)	0.6 (0.5)
	Isopoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.4 (0.2)
	Lepidoptera	4.1 (1.1)	13.9 (0.1)	0.0 (0.0)	0.0 (0.0)
	Neuroptera	0.4 (0.2)	0.9 (0.1)	0.0 (0.0)	0.0 (0.0)
	Opiliones	<0.1 (0.1)	0.2 (<0.1)	0.0 (0.0)	0.3 (0.1)
	Orthoptera	0.5 (0.1)	0.0 (0.0)	0.0 (0.0)	1.2 (0.3)
	Polydesemida	0.0 (0.0)	1.7 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Pscoptera	0.3 (1.3)	0.2 (0.4)	0.0 (0.0)	<0.1 (0.1)
	Thysanura	<0.1 (0.2)	<0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Unknown				
	Coleoptera	1.4 (2.2)	0.4 (0.2)	0.3 (0.4)	0.8 (0.9)
	Diptera	7.6 (53.7)	4.4 (0.7)	0.2 (0.6)	0.6 (0.6)
	Miscellaneous	0.0 (0.0)	17.5 (<0.1)	<0.1 (0.1)	0.0 (0.0)

Table A.9. Seasonal changes in taxonomic composition (mg dry mass•fish⁻¹) of invertebrates ingested by coastal cutthroat trout in deciduous, conifer, and mixed stream study sections of the Oregon Coast Range from July 2001 through April 2002. Numbers in parentheses indicate abundance (organisms•fish⁻¹).

Vegetation	Taxa	Summer	Fall	Winter	Spring
Deciduous	Aquatic				
	Acari	<0.1 (<0.1)	<0.1 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)
	Coleoptera	0.2 (0.1)	<0.1 (<0.1)	0.5 (0.1)	0.2 (0.1)
	Decapoda	0.0 (0.0)	1.4 (0.1)	1.3 (<0.1)	0.0 (0.0)
	Diptera	1.5 (2.2)	0.8 (2.0)	1.2 (3.2)	4.6 (25.6)
	Ephemeroptera	1.6 (2.1)	1.2 (1.3)	1.9 (2.0)	7.3 (7.8)
	Gastropoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	<0.1 (<0.1)
	Hemiptera	<0.1 (0.1)	0.3 (<0.1)	0.0 (0.0)	<0.1 (0.1)
	Neuroptera	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Plecoptera	5.3 (0.8)	1.6 (0.3)	1.8 (0.8)	4.6 (1.9)
	Trichoptera	3.1 (2.3)	2.5 (1.4)	4.2 (1.9)	3.8 (3.8)
	Terrestrial				
	Araneida	1.0 (0.4)	1.9 (0.5)	0.6 (0.1)	1.0 (0.5)
	Chelonethida	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	<0.1 (<0.1)
	Chordeumida	0.2 (<0.1)	<0.1 (<0.1)	<0.1 (<0.1)	0.0 (0.0)
	Coleoptera	2.2 (0.5)	0.9 (0.3)	<0.1 (<0.1)	4.1 (1.5)
	Collembola	<0.1 (0.1)	<0.1 (0.4)	<0.1 (0.1)	<0.1 (0.3)
	Diptera	4.0 (0.9)	0.2 (0.3)	<0.1 (<0.1)	0.3 (1.1)
	Gastropoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Geophilomorpha	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.9 (<0.1)
	Hemiptera	0.2 (<0.1)	0.1 (<0.1)	0.1 (<0.1)	<0.1 (<0.1)
	Homoptera	2.0 (0.7)	1.8 (0.6)	0.0 (0.0)	1.3 (0.4)
	Hymenoptera	0.6 (0.4)	0.7 (1.8)	0.0 (0.0)	0.1 (0.1)
	Isopoda	<0.1 (<0.1)	0.1 (<0.1)	0.0 (0.0)	0.1 (0.1)
	Isoptera	0.0 (0.0)	0.4 (0.1)	0.0 (0.0)	0.0 (0.0)
	Lepidoptera	0.1 (<0.1)	0.6 (0.1)	0.0 (0.0)	0.4 (0.2)
	Neuroptera	0.1 (0.1)	<0.1 (<0.1)	0.0 (0.0)	0.1 (<0.1)
	Opiliones	<0.1 (<0.1)	<0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Orthoptera	1.9 (<0.1)	3.5 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Polydesmida	0.3 (0.1)	1.5 (0.1)	0.0 (0.0)	0.0 (0.0)
	Pscoptera	<0.1 (<0.1)	<0.1 (0.1)	0.0 (0.0)	0.0 (0.0)
	Thysanura	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	<0.1 (<0.1)
	Unknown				
	Coleoptera	0.8 (0.3)	0.1 (0.1)	0.6 (<0.1)	0.1 (0.1)
	Collembola	0.1 (<0.1)	<0.1 (<0.1)	0.1 (<0.1)	<0.1 (0.1)
	Diptera	0.2 (0.6)	0.2 (0.8)	0.0 (0.0)	0.1 (0.3)
	Oligochaeta	0.1 (0.1)	0.0 (0.0)	0.5 (0.3)	0.4 (<0.1)

Vegetation	Taxa	Summer	Fall	Winter	Spring
Conifer	Aquatic				
	Acari	<0.1 (<0.1)	<0.1 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)
	Coleoptera	<0.1 (<0.1)	0.1 (0.1)	0.1 (0.1)	<0.1 (0.1)
	Decapoda	1.3 (<0.1)	1.4 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Diptera	0.1 (0.8)	0.1 (0.6)	1.7 (1.5)	2.9 (5.5)
	Ephemeroptera	1.3 (<0.1)	0.4 (1.3)	1.9 (1.9)	9.8 (6.4)
	Gastropoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Hemiptera	0.4 (<0.1)	<0.1 (<0.1)	0.7 (<0.1)	0.0 (0.0)
	Neuroptera	0.0 (0.0)	0.2 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Plecoptera	0.8 (0.7)	2.1 (0.5)	0.5 (0.6)	4.4 (1.8)
	Trichoptera	1.0 (0.9)	0.5 (0.6)	3.6 (2.6)	5.4 (3.7)
	Terrestrial				
	Araneida	0.2 (0.2)	1.8 (0.2)	0.1 (0.1)	2.9 (0.6)
	Chelonethida	0.0 (0.0)	0.0 (0.0)	<0.1 (<0.1)	<0.1 (<0.1)
	Chordeumida	0.1 (<0.1)	0.1 (<0.1)	<0.1 (<0.1)	<0.1 (<0.1)
	Coleoptera	1.3 (0.2)	1.8 (0.1)	0.2 (0.1)	2.4 (0.8)
	Collembola	<0.1 (<0.1)	<0.1 (0.1)	<0.1 (<0.1)	<0.1 (0.2)
	Diptera	0.7 (0.2)	<0.1 (0.1)	<0.1 (0.1)	<0.1 (<0.1)
	Gastropoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.1 (<0.1)
	Geophilomorpha	0.1 (<0.1)	0.0 (0.0)	<0.1 (<0.1)	0.0 (0.0)
	Hemiptera	0.3 (<0.1)	0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Homoptera	0.7 (0.2)	0.1 (<0.1)	0.1 (0.1)	1.4 (0.4)
	Hymenoptera	0.2 (0.1)	0.2 (0.5)	0.0 (0.0)	0.1 (<0.1)
	Isopoda	0.0 (0.0)	<0.1 (<0.1)	0.1 (<0.1)	0.2 (0.1)
	Isoptera	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Lepidoptera	0.3 (<0.1)	0.9 (<0.1)	<0.1 (0.1)	0.3 (0.1)
	Neuroptera	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Opiliones	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Orthoptera	0.9 (<0.1)	0.4 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Polydesemida	2.0 (0.0)	1.0 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Pscoptera	0.0 (0.0)	<0.1 (0.2)	0.0 (0.0)	0.0 (0.0)
	Thysanura	<0.1 (<0.1)	0.3 (0.1)	0.0 (0.0)	<0.1 (<0.1)
	Unknown				
	Coleoptera	1.8 (0.3)	<0.1 (0.1)	0.1 (0.1)	0.2 (0.1)
	Collembola	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	<0.1 (0.1)
	Diptera	0.2 (0.2)	<0.1 (0.1)	0.0 (0.0)	0.2 (0.2)
	Oligochaeta	0.0 (0.0)	0.0 (0.0)	2.9 (0.2)	6.4 (1.2)
Mixed	Aquatic				
	Acari	0.1 (0.1)	0.0 (0.0)	<0.1 (<0.1)	<0.1 (<0.1)
	Coleoptera	0.4 (0.2)	0.1 (0.1)	0.5 (0.1)	0.4 (0.2)

Vegetation	Taxa	Summer	Fall	Winter	Spring
	Decapoda	0.2 (<0.1)	0.5 (0.1)	0.0 (0.0)	0.0 (0.0)
	Diptera	0.8 (3.1)	0.1 (1.0)	0.3 (1.6)	2.7 (7.4)
	Ephemeroptera	2.8 (5.2)	0.6 (1.2)	1.0 (1.5)	13.3 (9.7)
	Gastropoda	0.0 (0.0)	0.0 (0.0)	<0.1 (<0.1)	0.0 (0.0)
	Hemiptera	0.1 (<0.1)	<0.1 (<0.1)	1.1 (<0.1)	0.2 (0.2)
	Neuroptera	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Plecoptera	0.7 (1.0)	0.6 (0.3)	1.4 (1.1)	3.9 (2.7)
	Trichoptera	1.6 (1.2)	0.4 (0.6)	1.1 (1.0)	5.3 (3.3)
	Terrestrial				
	Araneida	0.5 (0.3)	1.0 (0.3)	<0.1 (<0.1)	0.1 (0.1)
	Chelonethida	0.0 (0.0)	<0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Chordeumida	0.0 (0.0)	1.8 (0.1)	0.0 (0.0)	0.0 (0.0)
	Coleoptera	0.7 (0.3)	0.3 (0.5)	<0.1 (0.1)	2.8 (0.6)
	Collembola	<0.1 (0.3)	<0.1 (0.1)	<0.1 (0.1)	<0.1 (0.1)
	Diptera	0.6 (0.4)	0.1 (0.2)	<0.1 (<0.1)	<0.1 (0.1)
	Gastropoda	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Geophilomorpha	0.0 (0.0)	0.4 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Hemiptera	<0.1 (<0.1)	0.2 (<0.1)	0.0 (0.0)	0.0 (0.0)
	Homoptera	0.6 (0.5)	0.3 (0.3)	<0.1 (<0.1)	0.8 (0.2)
	Hymenoptera	1.0 (0.5)	0.2 (0.2)	0.1 (<0.1)	<0.1 (0.1)
	Isopoda	0.0 (<0.1)	<0.1 (<0.1)	0.0 (0.0)	0.4 (0.1)
	Isoptera	0.0 (0.0)	0.0 (0.0)	0.1 (<0.1)	0.0 (0.0)
	Lepidoptera	0.3 (0.1)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)
	Neuroptera	<0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Opiliones	<0.1 (<0.1)	0.3 (0.1)	0.0 (0.0)	0.0 (0.0)
	Orthoptera	2.0 (0.1)	5.7 (0.1)	0.0 (0.0)	0.0 (0.0)
	Polydesemida	0.1 (0.1)	1.3 (0.2)	0.0 (0.0)	0.0 (0.0)
	Psocoptera	0.1 (0.4)	<0.1 (0.2)	0.0 (0.0)	0.0 (0.0)
	Thysanura	<0.1 (<0.1)	0.0 (0.0)	0.0 (0.0)	<0.1 (<0.1)
	Unknown				
	Coleoptera	1.0 (0.3)	<0.1 (0.1)	0.0 (0.0)	0.1 (0.1)
	Collembola	<0.1 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)	<0.1 (<0.1)
	Diptera	0.2 (0.5)	<0.1 (0.1)	0.2 (0.1)	<0.1 (0.1)
	Oligochaeta	0.0 (0.0)	0.0 (0.0)	<0.1 (0.1)	0.1 (<0.1)